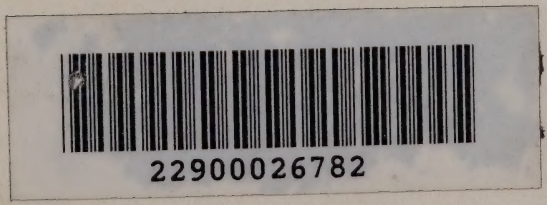
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CARPENTER'S

PRINCIPLES

OF

HUMAN PHYSIOLOGY

EDITED BY

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SURGEON TO THE ROYAL WESTMINSTER OPHTHALMIC HOSPITAL

Ninth Edition

LONDON
J. & A. CHURCHILL, NEW BURLINGTON STREET
1881

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EDITOR'S PREFACE.

In the preparation of this Edition the general arrangement of the work has been preserved, except that the sections on Pathology have been condensed, partly with the view of reducing the size of the volume, and partly because large treatises are now devoted to this subject, which, when the earlier editions of the work were published, was still in its infancy. Every page has undergone revision, and to some paragraphs considerable additions have been made.

In Physiological Chemistry the standard works of Hoppe-Seyler and of Hofmann have been taken as guides; and the Editor regrets that the valuable treatise of Professor Gamgee appeared too recently to enable him to make use of it in the preparation of the sections on this subject.

In Histology the treatises of Ranvier, Frey, Toldt and Krause, and the excellent Atlas in course of publication by Klein and Noble Smith, have been chiefly consulted.

In the purely Physiological sections an endeavour has been made to introduce in short compass the results of the more important Physiological work that has been done during the last three or four years. The statements made have generally been taken from the original articles, but in some instances the careful abstracts contained in Schmidt's "Jahrbuch," the "Centralblatt für die Medicinischen Wissenschäften," and in the "Medical Record," have been taken as the authorities. The value of such abstracts, made by competent men, increases constantly with the ever-increasing number of journals and memoirs, which has now become so great as to render it almost impossible for the most indefatigable to read all. This is especially

the case with the long and exhaustive memoirs of the Germans, correct and short abstracts of which are particularly useful.

I have to thank my son, Mr. D'Arcy Power, for working up the chapter on Development, for revising many of the sheets, and for aid in completing the Index, which, it is hoped, will be found unusually complete and accurate.

The student must not expect to learn Physiology from such a work as this. Physiology is now, as Anatomy has always been, a practical subject, and just as a competent knowledge of Anatomy can only be acquired in the dissecting-room, so Physiology can only be learned in the laboratory. The institution of such laboratories by Sharpey, Foster, Sanderson, Rolleston, Rutherford, Gamgee, and many others, in connection with the universities or with medical schools, enables every one to commence the study of Physiology at the beginning under competent instruction, and by familiarizing himself with the simplest, prepare himself to understand the more complex phenomena of life. All who are practically engaged in teaching feel that a sound knowledge of the elementary truths of Physiology is of far greater value to the practitioner than a superficial and necessarily inaccurate acquaintance with the hypotheses that are constantly being advanced, and as constantly modified or subverted.

The performance of experiments on living animals, even of a painless nature, has been practically abolished by the Legislature, but there still remains in the investigation of the phenomena of Development, in those of Histology and of Physiological Chemistry, wide fields of research for the original investigator; and the observations of Darwin, Cohn, and others, show how much may be learnt from an examination of the life history of plants, and of the lower forms of animal life, that is interesting to the student of human Physiology. It is upon such foundation, the value of which has only recently been clearly perceived, that Physiology must rest; and the more certainly the elementary facts are known, the more reliable and satisfactory will be all subsequent work.

HENRY POWER.

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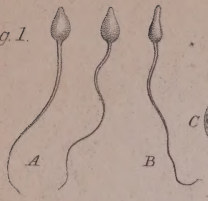

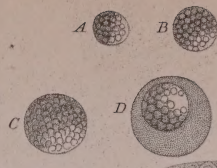

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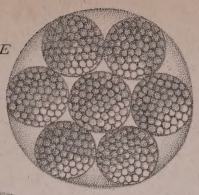

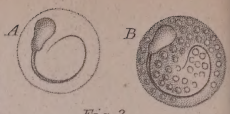

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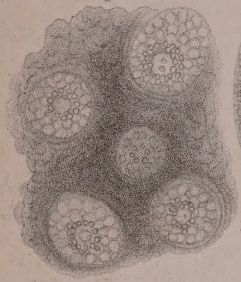

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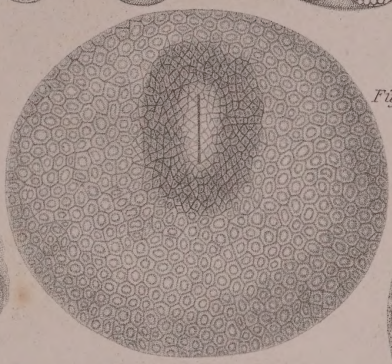

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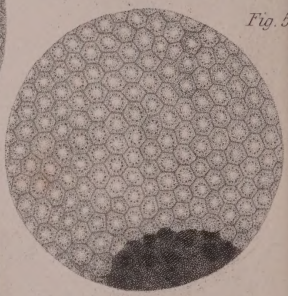

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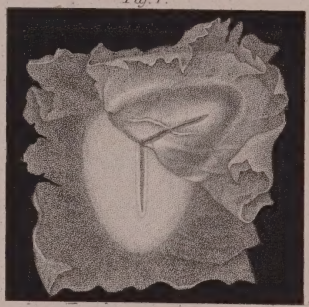

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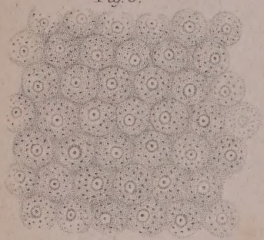

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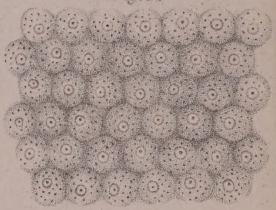

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FIG.

1. Spermatozoa of Man; A, viewed on the surface; B, viewed edgeways (§ 690).

2. Vesicles of evolution from the seminal fluid of the Dog; A, B, C, single vesicles of different sizes; D, single vesicle within its parent-cell; E, parent-cell enclosing seven vesicles of evolution (§ 691).

3. Development of Spermatozoa within the vesicles of evolution: A, B, vesicles containing spermatozoa in process of formation; C, D, spermatozoa escaping from the vesicles (§ 691).

[The three preceding figures are after Wagner and Leuckardt ("Cyclop. of Anatomy and Physiology," Art. 'Semen.')]

4. Thin slice of the ovarium of a Sow three weeks old, showing the Graafian vesicles or ovisacs imbedded in a fibro-cellular stroma. The ovisacs are filled with cells, in the midst of which one large one may be especially distinguished; this, which is the germinal vesicle, is surrounded by minute granules, which constitute the first indication of the yolk (§ 696).

5. Ovum of a Rabbit, showing the vitelline mass almost entirely converted into distinct cells, of which those at the surface are pressed against each other and against the zona pellucida, so as to assume a hexagonal form. The dark portion consists of a mass of vitelline spheres, which has not undergone this conversion (§ 696).

6. Ovum of the Rabbit, seven days after impregnation, viewed on a black ground. The outer membrane is the chorion, on which are seen incipient villosities. Within this is the *blastodermic vesicle*, at the summit of which is the projection formed by the *area germinativa;* and from this, the mucous layer of the germinal membrane is seen to extend over about one-third of the surface of the contained yolk (§ 733).

7. Portion of the germinal membrane, taken from the *area germinativa*, to show the two layers of which it is composed; the *serous*, or animal layer (epiblast) is turned back, so as to show the *mucous* or vegetative layer (mesoblast and hypoblast) *in situ*. In the latter is seen the *primitive trace* (§ 733).

8. Portion of the *serous* layer of the germinal membrane, highly magnified; showing that it is made-up of nucleated cells, united by intercellular substance, and filled with minute molecules (§ 733).

FIG.

9. Portion of the *mucous* layer of the germinal membrane, highly magnified; showing that it is made-up of cells, whose borders are more distinct and more closely applied to each other than those of the serous layer, and whose contents are more transparent (§ 733).

[The six preceding figures are after Bischoff ("Entwickelungsgeschichte der Säugethiere," &c. (1842)—"das Kaninchen-eies"—(1842)—"des Hunde-eies" (1845).]

10. Gravid Uterus of a Woman who had committed suicide in the seventh week of pregnancy, laid open:—*a*, os uteri internum; *b*, cavity of the cervix; *c*, *c*, *c*, *c*, the four flaps of the body of the uterus turned back; *d*, *d*, *d*, inner surface of uterine decidua; *e*, *e*, decidua reflexa; *f*, *f*, external villous surface of the chorion; *g*, internal surface of the chorion; *h*, amnion; *i*, umbilical vesicle; *k*, umbilical cord; *l*, embryo; *m*, space between chorion and amnion (§ 710 *et seq.*). [After Wagner ("Icones Physiologicæ").]

PLATE II.

11. Uterine Ovum of Rabbit, showing the Area Pellucida, with the primitive trace (§§ 733, 734).

12. More advanced Ovum, showing the incipient formation of the Vertebral column, and the dilatation of the primitive groove at its anterior extremity (§ 733).

13. More advanced Embryo, seen on its ventral side, and showing the first development of the Circulating apparatus. Around the Vascular Area is shown the terminal sinus *a*, *a*, *a*. The blood returns from this by two superior branches, *b*, *b*, and two inferior, *c*, *c*, of the omphalo-mesaraic veins, to the heart, *d*; which is, at this period, a tube curved on itself, and presenting the first indication of a division into cavities. The two aortic trunks appear, in the abdominal region, as the inferior vertebral arteries, *e*, *e*; from which are given off the omphalo-mesaraic arteries, *f*, *f*, which form a network that distributes the blood over the vascular area. In the cephalic region are seen the anterior cerebral vesicles, with the two ocular vesicles, *g* (§ 735).

(The three preceding figures are from the works of Bischoff previously cited.]

PLATE III.

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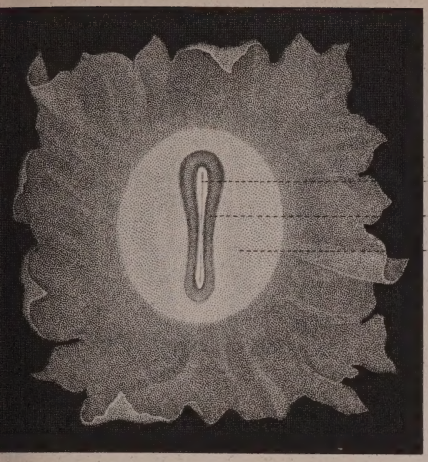
Comparative View of the Skeleton of Man, and that of the Orang Outan. [After Owen ("Zoological Transactions," vol. i.).]

Fig. 11.



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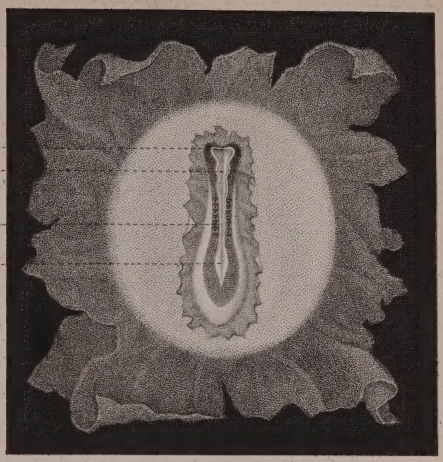

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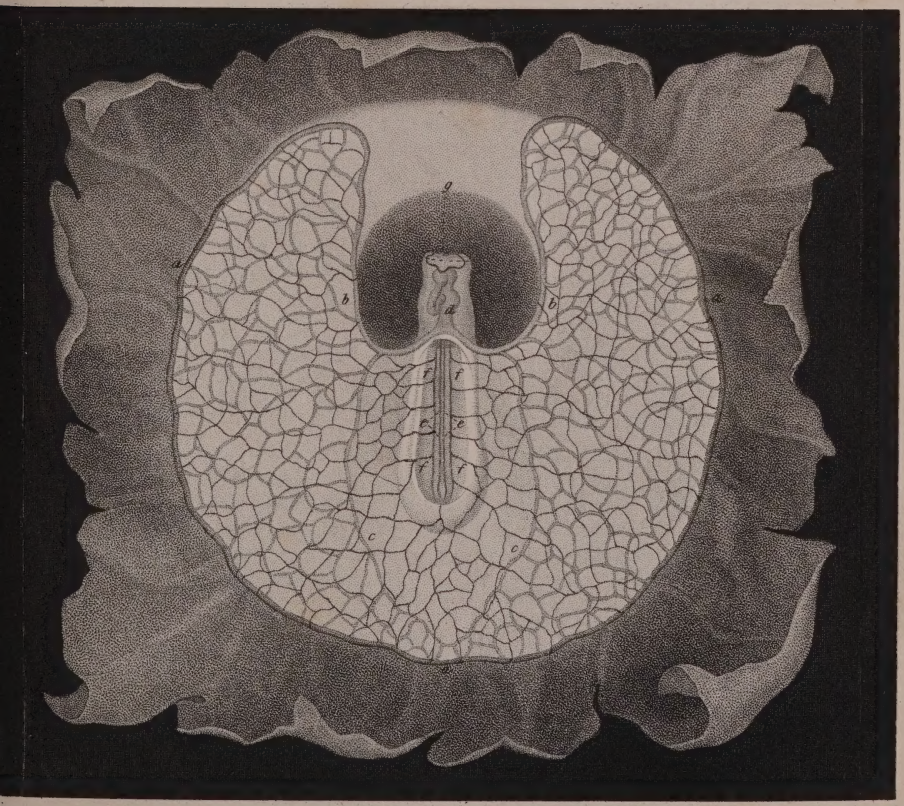

H.Adlard Sc.

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CHAPTER I.

OF LIFE, AND ITS CONDITIONS.

1. The term *Life* has been used by different writers, Physiological and Ontological, in a great variety of significations; but these are for the most part capable of reduction to three categories,—Life being regarded either (1) as the *aggregate of the phenomena* exhibited by any Organized being from the commencement to the conclusion of its individual existence, or (2) as the *mode of activity* peculiar to such beings, whereby they are distinguished from inanimate bodies, or (3) as the *special agency* supposed to be inherent in every organism, and to be the efficient cause alike of its first development and of its subsequent maintenance. The first is the sense in which the term is understood by Philosophers of the 'positive' school, who refuse to concern themselves with anything save phenomena that are immediately cognizable by the senses: while the last is the meaning attached to it by such as think that a great deal of trouble is saved by the assumption of a hypothetical entity, whose agency may at once account for everything not to be otherwise explained. To both these definitions it may be objected that they tend to limit inquiry into the essential nature of Vital Action. For by taking the former as a starting-point, we are led to fix our attention too exclusively on the *material conditions* presented in the structure of the Organism, and to ignore the *forces* by which its activity is maintained: just as if, in studying the operations of a Cotton-factory, we were to limit our attention to the mechanism of the carding, spinning, weaving, and other machines by whose instrumentality its products are elaborated, and were to neglect, as a condition not directly cognizable by our senses, the Motive Power without which those machines would all be inert. On the other hand, by resting in the assumption of a "Vital Principle" or "Organic Agent" as affording a sufficient account of all that is mysterious in the nature of Life, we really remove it from the domain of scientific inquiry; just as if the visitor to a Cotton-factory were to give up in despair any attempt to acquaint himself with the meaning of the several processes that go on before his eyes, and were to regard it as a sufficient account of the transformation of raw cotton into woven calico, that it takes place by the agency of a "calico-making principle."

2. But if, on the other hand, the Physiologist takes as his stand-point the conception of Life as *a peculiar mode of activity*, he at once finds himself on a pathway of inquiry marked out for him by the antecedent researches of the Physical philosopher. For as, in the study of that great cycle of mutually-related changes which may be designated the Life of the Universe, the Physicist has been led in the first instance to recognise several distinct modes of activity, *e.g.*, Mechanical and Chemical, Electrical and Thermal; and then, prosecuting his analysis under the guidance of that idea of Power which he finds in his own sense of effort, has been brought to refer every effect to a causative Force of some kind, acting through a certain Material instrumentality:—so the Physio-

logist who makes the living Organism his study, is led in the first place to refer its peculiar phenomena to a set of categories as distinct from the preceding as they are from each other; and thence to distinguish between their *instrumental* and their *dynamical* conditions, the Organic Structure and the Vital Forces which animate it. But further, as the Physicist, in proportion to the elevation of his stand-point and the comprehensiveness of the survey he can thence take of the phenomena of the Inorganic Universe, is enabled to discern, first the mutual relation, and at last the essential unity, of all those Forces whose manifestations appeared so diverse when separately contrasted: so may the Physiologist, in proportion to the insight he gains into the peculiar characteristics of Vital Activity, come in the first instance to recognise the mutual relation of the agencies which underlie its diversified phenomena, next to perceive their fundamental unity as so many expressions of one and the same Vital Force acting through different material instrumentalities, and finally to discern the essential identity of this Force with that which maintains the ceaseless cycle of activity in the Universe at large.*

3. If, now, we inquire what it is that essentially distinguishes Vital from every kind of Physical Activity, we find this distinction most characteristically expressed in the fact, that a germ endowed with Life develops itself into an Organism of a type resembling that of its parent; that this organism is the subject of incessant changes, which all tend in the first place to the evolution of its typical form, and subsequently to its maintenance in that form, notwithstanding the antagonism of Chemical and Physical agencies which are continually tending to produce its disintegration; but that, as its term of existence is prolonged, its conservative power declines, so as to become less and less able to resist these disintegrating forces, to which it finally succumbs, leaving the organism to be resolved by their agency into the components from which its materials were originally drawn. The history of a Living Organism, then, is one of *incessant change*;† and the conditions of this change are to be found partly in the organism itself, and partly in the external agencies to which it is subjected.

4. But the Life of any complex organism, such as that of Man, is the aggregate of the Vital Activity of all its component parts; and we must ascertain the conditions on which the activity of each of these is dependent, before we can rightly comprehend their united action in the Life of the whole. No fact has been more clearly ascertained by modern Physiological research than this,—that as the germ derives from its parent certain independent endowments, in virtue of which it is enabled to develop itself (under appropriate conditions) into an organism which may be composed of a vast number of dissimilar parts,

* See the Author's Memoir 'On the Mutual Relations of the Vital and Physical Forces,' in the "Philosophical Transactions" for 1850.

† If change be essential to our idea of Life, it may be asked what is the condition of a Seed, which may remain unaltered during a period of many centuries, vegetating at last, when placed in favourable circumstances, as if it had only ripened the year before. We can scarcely call it *alive*, for it is not performing any vital operation. But it is not *dead;* for it has undergone no disintegration, and retains its *capacity for living*, which is analogous to the *potential energy* of the Physicist. The most correct designation of such a state (which can only be maintained under a complete seclusion from disintegrating agencies) seems to be *dormant vitality*. Certain Animals may be reduced to it; as the Frog by cold, and the Wheel-animalcule by slow desiccation. Organisms capable of undergoing such a suspension of activity may be kept in a dormant condition so long as disintegrating agencies are excluded; but the very conditions (as heat in the one case, moisture in the other, and both combined in the case of the seed) whose presence is followed by the renewal of active life if the organism has undergone no injurious change, insure its speedy decay if it be not able to resume its proper vital activity.

so each of those parts derives from the germ in which it had its origin an independent capacity for development and maintenance, in virtue of which it goes through its own course of vital activity, and by the ultimate cessation of which its own term of existence is limited. Of this mutual independence we have illustrations in the persistence of the 'molecular life' of individual parts long after 'somatic' death (or death of the body as a whole) has taken place;—in the fact that not only may vital activity be sustained in a part completely separated from the body by the maintenance of the circulation of blood through it, but vital endowments which had partially or completely ceased to manifest themselves in consequence of the cessation of the circulation, may be restored by its re-establishment;—and in the occasional reunion of members which have been entirely separated. But notwithstanding the wonderful diversity of structure and of endowments which we meet with in the study of any such complex organism, we encounter a harmonious unity or co-ordination in its entire aggregate of actions, which is yet more wonderful. It is in this harmony of co-ordination, whose tendency is to the conservation of the organism, that the state of Health or Normal Life essentially consists. And the more profound is our investigation of its conditions, the more definite becomes the conclusion to which we are led by the study of them,—that it is fundamentally based on the common origin of all these diversified parts in the same germ; the vital endowments of which, equally diffused throughout the whole fabric in those lowest forms of organization in which every part is but a repetition of every other, are differentiated in the highest amongst a variety of organs or instrumental structures more or less dissimilar, acquiring in virtue of this differentiation a much greater intensity.

5. In the lowest forms of Vegetable life, the primordial germ multiplies itself by duplicative subdivision into an apparently unlimited number of cells, each of them similar to every other, and capable of maintaining its existence independently of them. And in that lowest (Rhizopod) type of Animal life, the knowledge of which is among the most remarkable fruits of modern biological research, "the Physiologist has a case in which those vital operations which he is elsewhere accustomed to see carried on by an elaborate apparatus, are performed without any special instruments whatever; a little particle of apparently homogeneous jelly changing itself into a greater variety of forms than the fabled Proteus, laying hold of its food without members, swallowing it without a mouth, digesting it without a stomach, appropriatiug its nutritious material without absorbent vessels or a circulating system, moving from place to place without muscles, feeling (if it has any power to do so) without nerves, propagating itself without genital apparatus, and not only this, but in many instances forming shelly coverings of a symmetry and complexity not surpassed by those of any testaceous animals;"* whilst the mere separation of a fragment of this jelly is sufficient to originate a new and independent organism, so that any number of these beings may be produced by the successive detachment of such particles from a single Rhizopod, each of them retaining (so far as we have at present the means of knowing) the characteristic endowments of the stock from which it was an offset.

6. When, on the other hand, we watch the evolution of any of the higher types of Organization, whether Vegetable or Animal, we observe that although in the first instance the primordial cell multiplies itself by duplicative subdivision into an aggregation of cells which are apparently but repetitions of itself and of each other, this homogeneous extension has in each case a definite

* See the Author's "Introduction to the Study of the Foraminifera," published by the Ray Society, 1862, Preface, p. vii.

limit, speedily giving place to a structural differentiation which becomes more and more decided with the progress of development; until, in that most heterogeneous of all types—the Human Organism—no two parts are precisely identical, except those which correspond to each other on the opposite sides of the body. With this structural differentiation is associated a corresponding differentiation of function; for whilst in the Life of the most highly-developed and complex organism, we witness no act which is not foreshadowed, however vaguely, in that of the lowest and simplest, yet we observe in it that same "division of labour" which constitutes the essential characteristic of the highest grade of Civilization. For in what may be termed the elementary form of Human Society, in which every individual relies upon himself alone for the supply of all his wants, no greater result can be attained by the aggregate action of the entire community, than its mere maintenance; but as each individual selects a special mode of activity for himself, and aims at improvement in that speciality, he finds himself attaining a higher and yet higher degree of aptitude for it; and this specialization tends to increase as opportunities arise for new modes of activity, until that complex fabric is evolved which constitutes the most developed form of the Social State, wherein every individual finds the work—mental or bodily—for which he is best fitted, and in which he may reach the highest attainable perfection; while the mutual dependence of the whole (which is the necessary result of this specialization of parts) is such that every individual works for the benefit of all his fellows, as well as for his own. As it is only in such a state of Society that the greatest triumphs of Human ability become possible, so it is only in the most differentiated types of Organization that Vital Activity can present its highest manifestations. In the one case as in the other does the result depend upon a process of gradual *development*, in which, under the influence of agencies whose nature constitutes a proper object of scientific inquiry, that *most general* form in which the fabric—whether Corporeal or Social—originates, evolves itself into that *most special* in which its development culminates. And hence we are distinctly justified in the conclusion, that the special endowments of the several components of the organism, however dissimilar to each other, are nothing else than differentiated and proportionately intensified expressions of those which are common to every part of the originally homogeneous fabric;—a conclusion which derives a remarkable confirmation from the indication afforded by the phenomenon of 'Metastasis of Secretion,' that the general structure, even in the most highly-specialized organism, retains somewhat of its primitive community of function.

7. Thus, then, we may take that mode of Vital Activity which manifests itself in the Evolution of the germ into the complete organism repeating the type of its parent, and in the subsequent maintenance of that organism in its integrity,—in both cases at the expense of materials derived from external sources,—as the most universal and most fundamental characteristic of Life; and we have now to consider the nature and source of the Force or Power by which that evolution is brought about. The prevalent opinion has until lately been, that this power is inherent in the germ; which has been supposed to derive from its parent not merely its material substance, but a *nisus formativus*, *bildungs-trieb*, or *germ-force*, in virtue of which it builds itself up into the likeness of its parent, and maintains itself in that likeness until the force is exhausted, at the same time imparting a fraction of it to each of its progeny. In this mode of viewing the subject, all the organizing force required to build up an Oak or a Palm, an Elephant or a Whale, must be concentrated in a minute particle only discernible by microscopic aid; and

the aggregate of all the germ-forces appertaining to the descendants, however numerous, of a common parentage, must have existed in their original progenitors. Thus, in the case of the successive viviparous broods of *Aphides*, a germ-force capable of organizing a mass of living structure, which would amount (it has been calculated*) in the tenth brood to the bulk of 500 millions of stout men, must have been shut up in the single individual, weighing perhaps the 1-1000th of a grain, from which the first brood was evolved. A more complete *reductio ad absurdum* can scarcely be brought against any hypothesis; and we may consider it proved that, in some way or other, fresh organizing force is constantly being supplied *from without* during the whole period of the exercise of its activity. When we carefully look into the question, we find that what the *germ* really supplies is not the force, but the *directive agency;* thus rather resembling the control exercised by the superintendent builder who is charged with the working-out the design of the architect, than the bodily force of the workmen who labour under his guidance in the construction of the fabric. The actual constructive force, as we learn from an extensive survey of the phenomena of life, is supplied by Heat; the influence of which upon the rate of growth and development, both Animal and Vegetable, is so marked as to have universally attracted the attention of Physiologists; who, however, have for the most part only recognised in it a *vital stimulus* that calls forth the latent power of the germ, instead of looking upon it as itself furnishing the power that does the work.— It has been from the narrow limitation of the area over which Physiological research has been commonly prosecuted, that the intimacy of this relationship between Heat and the Organizing force has not sooner become apparent. Whilst the vital phenomena of Warm-blooded Animals, which possess within themselves the means of maintaining a constant temperature, were made the sole, or at any rate the chief objects of study, it was not likely that the inquirer would recognise the full influence of external Heat in accelerating, or of Cold in retarding, their functional activity. It is only when the survey is extended to Cold-blooded Animals, and to Plants, that the immediate and direct relation between Heat and Vital Activity, as manifested in the rate of growth and development, or of other changes peculiar to the living body, is unmistakably manifested. To some of those phenomena which afford the best illustrations of the mode in which Heat acts upon the living organism, attention will now be directed.

8. The agency of Heat as the 'efficient cause' or 'motive power' to which the phenomena of growth and development are to be referred, is peculiarly well seen in the process of Germination. The Seed consists of an embryo which has already advanced to a certain stage of development, and of a store of nutriment laid-up as the material for its further evolution; and in the fact that this evolution is carried on at the expense of organic compounds already prepared by extrinsic agency, until (the store of these being exhausted) the young plant is sufficiently far advanced in its development to be able to elaborate them for itself, the condition of the germinating embryo resembles that of an Animal. Now the seed, as already pointed out (§ 3, note), may remain (under favourable circumstances), in a state of absolute inaction during an unlimited period. If secluded from the free access of air and moisture, and kept at a low temperature, it is removed from all influences that would on the one hand occasion its disintegration, or on the other would call it into active life. But when again exposed to air and moisture, and

* See Prof. Huxley on the 'Agamic Reproduction of Aphis,' in "Linnæan Transactions," vol. xxii. p. 215.

subjected to a higher temperature, it either germinates or decays, according as the embryo it contains has or has not preserved its vital endowments,—a question which only experiment can resolve. The process of germination is by no means a simple one. The nutriment stored up in the seed is in great part in the condition of insoluble starch; and this must be brought into a soluble form before it can be appropriated by the embryo. The metamorphosis is effected by the agency of a ferment termed *diastase;* which is laid-up in the immediate neighbourhood of the embryo, and which, when brought to act on starch, converts it in the first instance into soluble dextrine, and then (if its action be continued) into sugar. The dextrine and sugar, combined with the albuminous and oily compounds also stored-up in the seed, are taken up by a process of intussusception contrasting strongly with the growth by apposition which characterizes the increase of a crystal, and form the 'protoplasm' which is the substance immediately supplied to the young plant as the material of its tissues; and the conversion of this protoplasm into various forms of organized tissue, which become more and more differentiated as development advances, is obviously referable to the vital activity of the germ. Now it can be very easily shown experimentally that the *rate of growth* in the germinating embryo is so closely related (within certain limits) to the amount of Heat supplied, as to place its dependence on that agency beyond reasonable question; so that we seem fully entitled to say that Heat, acting through the germ, becomes the constructive force or power by which the Vegetable fabric is built up.* But there appears to be another source of that power in the Seed itself. In the conversion of the insoluble starch of the Seed into sugar, and probably also in a further metamorphosis of a part of that sugar, a large quantity of carbon is eliminated, by combining with the oxygen of the air so as to form carbonic acid; this combination is necessarily attended with a disengagement of heat, which becomes very sensible when (as in malting) a large number of germinating seeds are aggregated together; and it cannot but be regarded as probable that the heat thus evolved within the seed concurs with that derived from without, in supplying to the germ the force that promotes its evolution.

9. The condition of the Plant which has attained a more advanced stage of its development, differs from that of the germinating embryo essentially in this particular, that the organic compounds which it requires as the materials of the extension of the fabric are formed by itself instead of being supplied to it from without. The tissues of the green surfaces of the leaves and stems, when acted on by light, have the peculiar power of generating at the expense of carbonic acid, water, and ammonia, various ternary and quarternary organic compounds, such as chlorophyll, starch, oil, and albumen; and of the compounds thus generated, some are appropriated by the constructive force of the Plant (derived from the heat with which it is supplied) to the formation of new tissues, whilst others are stored up in the cavities of those tissues, where they ultimately serve either for the evolution of parts subsequently developed, or for the nutrition of Animals which employ them as food. Of the source of those peculiar affinities by which the components of the Starch, Albumen, &c. are brought together, we have no

* The effect of Heat is doubtless manifested very differently by different seeds; such variations being partly *specific*, partly *individual*. But these are no greater than we see in the Inorganic world; the increment of temperature and the augmentation of bulk exhibited by different substances when subjected to the same absolute measure of heat, being as diverse as the substances themselves.—The whole process of 'malting,' it may be remarked, is based on the average regularity with which the seeds of a particular species may be at any time forced to a definite rate of germination by a definite increment of temperature.

right to speak confidently; but looking to the fact that these compounds are not produced in any case by the direct union of their elements, and that a decomposition of binary compounds seems to be a necessary antecedent of their formation, it is scarcely improbable that, as suggested by Prof. Le Conte,* that source is to be found in the chemical forces set free in the preliminary act of decomposition, in which the elements would be liberated in that 'nascent condition' which is well known to be one of peculiar energy. The influence of Light, then, upon the Vegetable organism appears to be essentially exerted in bringing about what may be considered a higher mode of chemical combination between oxygen, hydrogen, and carbon, with the addition of nitrogen, in certain cases; and there is no evidence that it extends beyond this. That the appropriation of the materials thus prepared, and their conversion into organized tissue in the operations of growth and development, are dependent on the agency of Heat, is just as evident in the stage of maturity as in that of germination. And there is reason to believe, further, that an additional source of Organizing force is to be found in the retrograde metamorphosis of organic compounds that goes on during the whole life of the plant; of which metamorphosis the expression is furnished by the production of carbonic acid. This is peculiarly remarkable in the case of the *Fungi*, which being incapable of forming new compounds under the influence of light, are entirely supported by the organic matters they absorb; corresponding in this respect on the one hand with the germinating Plant-embryo, and on the other with Animals. Such a decomposition of a portion of the absorbed material is the only conceivable source of the large quantity of carbonic acid they are constantly giving out; and it would not seem unlikely that the force supplied by this retrogade metamorphosis of the superfluous components of their food, which fall down (so to speak) from the elevated plane of 'proximate principles' to the lower level of comparatively simple binary compounds, constitutes the power by which another portion is raised to the rank of living tissue; thus accounting in some degree for the very rapid growth for which this tribe of Plants is so remarkable. This exhalation of carbonic acid, however, is not peculiar to Fungi and germinating embryos; for it takes place during the whole life of Flowering Plants, both by day and by night, in sunshine and in shade, and from their green as well as from their dark surfaces. It is not improbable that, as in the case of the Fungi, the source of this exhalation lies partly in the Organic matter absorbed; Plants being able to take up and assimilate soluble *humus*, which, being a more highly carbonized substance than starch, dextrine, or cellulose, can only be converted into compounds of the latter kind by parting with some of its carbon.† But it may also take place at the expense of compounds previously generated by the Plant itself, and stored up in its tissues, of which we seem to have an example in the unusual production of carbonic acid, which takes place at the period of flowering, especially in such plants as have a fleshy disk or receptacle containing a large quantity of starch; and thus, it may be surmised, an extra supply of force is provided for the maturation of those generative products, whose preparation seems to be the highest expression of the vital power of the Vegetable Organism.

10. The entire aggregate of Organic compounds contained in the Vegetable tissues, then, may be considered as the expression not merely of a

* See his very suggestive Memoir 'On the Correlation of Physical, Chemical, and Vital Force,' in the "Philosophical Magazine" for 1860, vol. xix. Ser. iv. p. 137.

† See the Memoir of M. Risler, 'On the Absorption of Humus,' in the "Bibliothèque Universelle," N.S., 1858, tom. i. p. 305.

certain amount of the *material elements* oxygen, hydrogen, carbon, and nitrogen derived (directly or indirectly) from the water, carbonic acid, and ammonia of the atmosphere, but also of a certain amount of *force* which has been exerted in raising these from the lower plane of simple binary compounds to the higher level of complex 'proximate principles;' whilst the portion of these actually converted into organized tissue may be considered as the expression of a further measure of force, which, acting under the directive agency of the germ, has served to build up the fabric in its characteristic type. This *constructive* action goes on during the whole Life of the Plant, which essentially manifests itself either in the extension of the original fabric (to which in many instances there seems no determinate limit), or in the production of the germs of new and independent organisms.—It is interesting to remark that the development of the more permanent parts involves the successional decay and renewal of parts whose existence is temporary; the 'fall of the leaf' being the effect, not the cause, of the cessation of that peculiar functional activity of its tissues, which consists in the elaboration of the nutritive material required for the production of wood. And it would seem as if the duration of the existence of such temporary parts stands in an inverse ratio to the energy of their action; the leaves of "evergreens," which are not cast off until the appearance of a new succession, effecting their functional changes at a much less rapid rate than do those of "deciduous" trees, whose term of life is far more brief.

11. Thus the final cause or purpose of the whole Vital Activity of the Plant, so far as the *individual* is concerned, is to produce an indefinite extension of the dense, woody, almost inert, but permanent portions of the fabric, by the successional development, decay, and renewal of the soft, active, and transitory cellular parenchyma; and, according to the principles already stated, the descent of a portion of the materials of the latter to the condition of binary compounds, which is manifested in the largely increased exhalation of carbonic acid that takes place from the leaves in the later part of the season, comes to the aid of external Heat in supplying the force by which another portion of those materials is raised to the condition of organized tissue.—The vital activity of the Plant, however, is further manifested in the provision made for the propagation of its race by the production of the germs of new individuals; and here, again, we observe that whilst a higher temperature than that which suffices to sustain the ordinary processes of vegetation, is usually required for the development of the flower and the maturation of the seed, a special provision appears to be made in some instances for the evolution of force in the sexual apparatus itself, by the retrograde metamorphosis of a portion of the organic compounds prepared by the previous nutritive operations. This seems the nearest approach presented in the Vegetable organism, to what we shall find to be an ordinary mode of activity in the Animal. That the performance of the generative act involves an extraordinary expenditure of Vital force, appears from this remarkable fact, that blossoms which wither and die as soon as the ovules have been fertilized, may be kept fresh for a long period if fertilization be prevented by cutting off the stamens before the bursting of the anthers.*

12. We are now prepared to inquire into the manifestations of Vital Activity in the Animal, and into the sources of the power by which the various forms of that activity are sustained. The first of these manifestations is, as in the Plant, the building up of the organism by the appropriation of

* On this subject see Herbert Spencer, "Principles of Biology," 1867, vol. ii. p. 419-470.

material supplied from external sources under the directive agency of the germ. The ovum of the Animal, like the seed of the Plant, contains a store of appropriate nutriment previously elaborated by the parent; and this store suffices for the development of the embryo, up to the period at which it can obtain and digest alimentary materials for itself. That period occurs in the different tribes of animals at very dissimilar stages of the entire developmental process. In many of the lower classes, the embryo comes forth from the egg, and commences its independent existence, in a condition which, as compared with the adult form, would be as if a Human embryo were thrown upon the world to obtain its own subsistence only a few weeks after conception; and its whole subsequent growth and development take place at the expense of the nutriment which the embryo ingests for itself. We have examples of this in the class of Insects, many of which come forth from the egg in the state of extremely simple and minute worms, having scarcely any power of movement, but an extraordinary voracity. The eggs having been deposited in situations fitted to afford an ample supply of appropriate nutriment (those of the flesh-fly, for example, being laid in carcases, and those of the cabbage-butterfly upon cabbage-leaves), each larva on its emersion is as well provided with alimentary material as if it had been furnished with a large supplemental yolk of its own; and by availing itself of this, it speedily grows to many hundred or even many thousand times its original size, without making any considerable advance in development. But having thus laid up in its tissues a large additional store of material, it passes into a state which, so far as the external manifestations of life are concerned, is one of torpor, but which is really one of great developmental activity; for it is during the *pupa* state that those new parts are evolved, which are characteristic of the perfect Insect, and of which scarcely a trace was discoverable in the larva; so that the assumption of this state may be likened in many respects to a re-entrance of the larva into the ovum. On its termination, the Imago or perfect Insect comes forth complete in all its parts, and soon manifests the locomotive and sensorial powers by which it is specially distinguished, and of which the extraordinary predominance seems to justify our regarding Insects as the types of purely *Animal* life. There are some Insects whose Imago-life has but a very short duration, the performance of the generative act being apparently the only object of this stage of their existence: and such for the most part take no food whatever after their final emersion, their vital activity being maintained, for the short period it endures, by the material assimilated during their larva state.* But those whose period of activity is prolonged, and upon whose energy there are extraordinary demands, are scarcely less voracious in their Imago than in their Larva-condition; the food they consume not being applied to the *increase* of their bodies, which grow very little after the assumption of the imago-state, but chiefly to their *maintenance*,—no inconsiderable portion of it, however, being appropriated in the female to the production of ova, the entire mass of which deposited by a single individual is sometimes enormous. That the performance of the generative act involves not merely a consumption of Material, but a special expenditure of Force, appears from a fact to be presently stated, corresponding to that already noticed (§ 11) in regard to Plants.

13. Now if we look for the source of the various kinds of Force,—which

* It is not a little curious that in the tribe of *Rotifera*, or Wheel-animalcules, all the males yet discovered are entirely *asplanchnic:* not only the whole of their development within the egg, but the whole of their active life after their emersion from it, being carried on at the expense of the store of yolk provided by the parent.

may be distinguished as constructive, sensori-motor, and generative,—that are manifested in the different stages of the life of an Insect, we find them to lie, on the one hand, in the Heat with which the organism is supplied from external sources, and, on the other, in the Food provided for it. The agency of heat, as the moving power of the constructive operations, is even more distinctly shown in the development of the Larva within the egg, and in the development of the Imago within its pupa-case, than it is in the germinating seed; the rate of each of these processes being strictly regulated by the temperature to which the organism is subjected. Thus ova which are ordinarily not hatched until the leaves suitable for the food of their larva have been put forth, may be made, by artificial heat, to produce a brood in the winter; whilst, on the other hand, if they be kept at a low temperature, their hatching may be retarded almost indefinitely without the destruction of their vitality. The same is true of the pupa-state; and it is remarkable that during the latter part of that state, in which the developmental process goes on with extraordinary rapidity, there is in certain Insects a special provision for an elevation of the temperature of the embryo by a process resembling incubation. Whether, in addition to the heat imparted from without, there is any addition of force developed within (as in the germinating seed) by the return of a part of the organic constituents of the food to the condition of binary compounds, cannot at present be stated with confidence: the probability is, however, that such a retrograde metamorphosis does take place, adequate evidence of its occurrence during the incubation of the Bird's egg being afforded by the liberation of carbonic acid which is there found to be an essential condition of the developmental process. During the larva-state there is very little power of maintaining an independent temperature, so that the sustenance of Vital Activity is still mainly due to the heat supplied from without.—But in the active state of the perfect Insect there is a *production of heat* quite comparable to that of warm-blooded animals; and this is effected by the retrograde metamorphosis of certain organic constituents of the food, of which we find the expression in the exhalation of carbonic acid and water. Thus the food of Animals becomes an internal source of heat, which may render them independent of external temperature.—Further, a like retrograde metamorphosis of certain constituents of the food is the source of that *sensori-motor power* which is the peculiar characteristic of the Animal organism; for on the one hand the demand for food, on the other the amount of metamorphosis indicated by the quantity of carbonic acid exhaled, bear a very close relation to the quantity of that power which is put forth. This relation is peculiarly manifest in Insects, since their conditions of activity and repose present a greater contrast in their respective rates of metamorphosis, than do those of any other animals.—Of the exercise of *generative* force we have no similar measure; but that it is only a special modification of ordinary vital activity appears from this circumstance, that the life of those Insects which ordinarily die very soon after sexual congress and the deposition of the ova, may be considerably prolonged if the sexes be kept apart so that congress cannot take place. Moreover, it has been shown by recent inquiries into the Agamic reproduction of Insects and other animals, that the process of Generation differs far less from those Reproductive acts which must be referred to the category of the ordinary Nutritive processes, than had been previously supposed.

14. Thus, then, we find that in the Animal organism the demand for food has reference not merely to its use as a *material* for the construction of the fabric; food serves also as a generator of *force;* and this force may be of

various kinds,—Heat and Motor-power being the principal but by no means the only modes under which it manifests itself. We shall now inquire what there is peculiar in the sources of the Vital Force which animates the organisms of the higher animals at different stages of Life.

15. That the Developmental force which occasions the evolution of the germ in the higher Vertebrata is really supplied by the heat to which the ovum is subjected, may be regarded as a fact established beyond all question. In the Frog and other Amphibia, which have no special means of imparting a high temperature to their eggs, the rate of development (which in the early stages can be readily determined with great exactness) is entirely governed by the degree of warmth to which the ovum is subjected. But in Serpents there is a peculiar provision for supplying heat; the female performing a kind of incubation upon her eggs, and generating in her own body a temperature much above that of the surrounding air.* In Birds, the developmental process can only be maintained by the steady application of external warmth, and this to a degree much higher than that which is needed in the case of cold-blooded animals; and we may notice two results of this application as very significant of the dynamical relation between Heat and Developmental Force,—first, that the period required for the evolution of the germ into the mature embryo is nearly constant, each species having a definite period of incubation,—and second, that the grade of development attained by the embryo before its emersion is relatively much higher than it is in cold-blooded vertebrata generally; the only instances in which anything like the same stage is attained without a special incubation being those in which (as in the Turtle and Crocodile) the eggs are hatched under the influence of a high external temperature. This higher development is attained at the expense of a much greater consumption of nutrient material; the store laid up in the 'food yolk' and 'albumen' of the Bird's egg being many times greater in proportion to the size of the animal which laid it, than that contained in the whole egg of a Frog or a Fish. There is evidence in that liberation of carbonic acid which has been ascertained to go on in the egg (as in the germinating seed) during the whole of the developmental process, that the return of a portion of the organic substances provided for the sustenance of the embryo, to the condition of simple binary compounds, is an essential condition of the process; and since it can scarcely be supposed that the object of this metamorphosis can be to furnish *heat* (an ample supply of that force being afforded by the body of the parent), it seems not unlikely that its purpose is to supply a force that concurs with the heat received from without in maintaining the process of organization

16. The development of the embryo within the body, in the Mammalia, imparts to it a steady temperature equivalent to that of the parent itself; and in all, save the *implacental* Orders of this class, that development is carried still further than in Birds, the new-born Mammal being yet more complete in all its parts, and its size bearing a larger proportion to that of its parent than even in Birds. It is doubtless owing in great part to the constancy of the temperature to which the embryo is subjected that its rate of development (as shown by the fixed term of utero-gestation) is so uniform. The supply of organizable material here afforded by the ovum itself is very small, and suffices only for the very earliest stage of the constructive process; but a special provision is

* In the Viper the eggs are usually retained within the oviduct until they are hatched. In a Python, which went through the process of incubation in the Zoological Gardens, the eggs were embedded in the coils of the body; the temperature to which they were subjected)as ascertained by a thermometer placed in the midst of them) averaging 90° F., whilst that of the cage averaged 60° F.

very soon made for the nutrition of the embryo by materials directly supplied by the parent; and the imbibition of these takes the place, during the whole remainder of fœtal life, of the appropriation of the materials supplied in the Bird's egg by the 'food yolk' and 'albumen.' To what extent a retrograde metamorphosis of nutrient material takes place in the fœtal Mammal we have no precise means of determining, since the products of that metamorphosis are probably for the most part returned (through the placental circulation) to the blood of the mother, and got rid of through her excretory apparatus. But sufficient evidence of such a metamorphosis is afforded by the presence of urea in the amniotic fluid, and of biliary matter in the intestines, to make it probable that it takes place not less actively (to say the least) in the fœtal Mammal than it does in the Chick in *ovo*. Indeed, it is impossible to conceive of the growth of any of the higher organisms—which not merely consists in the formation of new parts, but also involves a vast amount of interstitial change—without perceiving that in the remodelling which is incessantly going on the parts first formed must be removed to make way for those which have to take their place. And such removal can scarcely be accomplished without a retrograde metamorphosis which, as in the numerous cases already referred to, may be considered, with great probability, as setting free constructive force to be applied in the production of new tissue.

17. If, now, we pass on from the intra-uterine life of the Mammalian organism to that period of its existence which intervenes between birth and maturity, we see that a temporary provision is made in the acts of lactation and nursing for affording both food and warmth to the young creature, which is at first incapable of adequately providing itself with aliment, or of resisting external cold, without fostering aid. And we notice that the offspring of Man remains longer dependent upon parental care than that of any other Mammal, in accordance with the higher grade of development to be ultimately attained. But when the period of infancy has passed, the child that is adequately supplied with food, and is protected by the clothing which makes up for the deficiency of other tegumentary covering, ought to be able to maintain its own heat, save in an extremely depressed temperature; and this it does by the metamorphosis of organic substances, partly derived from its own fabric, and partly supplied directly by the food into binary compounds. During the whole period of growth and development we find the producing power at its highest point; the circulation of blood being more rapid, and the amount of carbonic gas generated and thrown off being much greater in proportion to the bulk of the body than at any subsequent period of life. We find, too, in the large amount of other excretions the evidence of a rapid metamorphosis of tissue; and it can hardly be questioned (if our general doctrines be well founded) that the constructive force which operates in the completion of the fabric will be derived in part from the heat so largely generated by chemical change, and in part from the descent which a portion of the fabric itself is continually making from the higher plane of organized tissue to the lower plane of dead matter. This high measure of vital activity can only be sustained by an ample supply of Food; which thus supplies both *material* for the construction of the organism, and the *force* by whose agency that construction is accomplished. How completely dependent the constructive or organizing process still is upon Heat is shown by the phenomena of reparation in cold-blooded animals; since not only can the rate at which they take place be experimentally shown to bear a direct relation to the temperature to which these animals are subjected, but it has been ascertained that any extraordinary act of reparation (such as the reproduction of a limb in the Salamander) will

only be performed under the influence of a temperature much higher than that required for the maintenance of the ordinary vital activity.

18. After the maturity of the Organism has been attained there is no longer any call for a larger measure of constructive force than is required for the *maintenance* of its integrity; and if there were no other source of retrograde metamorphosis than that which is inherent in the peculiar composition of the tissues, the demand for food would be reduced to very little more than would suffice, by its ultimate conversion into water and carbonic acid, to keep up the Temperature of the body. But the conditions of Animal existence involve a constant expenditure of *Motor* force through the instrumentality of the Nervo-muscular apparatus as well as a liberation of Heat; and the exercise of the purely *Psychical* powers through the instrumentality of the Brain constitutes a further expenditure of force, even when no bodily exertion is made as its result.—We have now to consider the conditions under which these forces are developed, and the sources from which they are derived.

19. That the Motor force which is put forth in the contraction of a Muscle is generated by the oxygenation of the component elements, either of the muscle itself, or of the blood which circulates through it, may be considered as demonstrated by these two facts—(1) that while the blood which circulates through a Muscle at rest is returned by its veins in an almost arterial condition, its hue changes to venous as soon as the muscle is thrown into action; and (2) that the quantity of carbonic acid exhaled bears a constant relation, *ceteris paribus*, to the amount of muscular exertion put forth, as has been especially shown by the experiments of Mr. Newport and Dr. Edward Smith —the former upon Insects, the latter on the Human subject. It is interesting to note the different ways in which this oxygenation is brought about in the two cases. In the Insect, the aëration is quite independent of the blood circulation; being provided for by the direct penetration of air, through the ramifications of the *tracheæ*, into the substance of the muscles. But in Man, as in Vertebrata generally, the Blood is not only the *nutrient*, but is also the *oxygenating* medium; and, while in the organic compounds with which it is charged it has a store of "potential energy," it is only by the presence of the free Oxygen which it carries with it that those changes can be maintained whereby "potential energy" is converted into "actual energy." When the doctrine now known as that of the "Conservation of Energy"* was first worked out in regard to the production of Animal Force, it was supposed that every exertion of muscular power involved a metamorphosis of the tissue of the muscle itself sufficient in its amount to produce the mechanical equivalent of the heat that would be otherwise liberated by the combustion of its Hydrocarbon. But the observations of MM. Fick and Wislicenus on the increase of the urea, and other nitrogenous products of the disintegration of muscle, which shows itself in the urine during and after prolonged muscular exertion

* The earliest distinct general expression of this doctrine is to be found in the very remarkable treatise of Dr. Mayer ("Die organische Bewegung in ihren Zusammenhange mit dem Stoffwechsel," *Heilbronn*, 1845), in which he worked-out from the two fundamental axioms, "*Ex nihilo nil fit*," and "*Nil fit ad nihilum*," the whole system of doctrine which has since come to be known as that of the "Correlation of Forces," and the "Conservation of Energy," in its application alike to Physics and Chemistry and to Physiology. Sir William Grove was simultaneously engaged in the development of the doctrine of the "Correlation of the Physical Forces" as Prof. Helmholtz was in that of the "Conservation of Energy;" and without any knowledge of the previous labours either of Dr. Mayer or of Prof. Helmholtz, the Author of this Treatise developed a similar doctrine in his Memoir 'On the Mutual Relations of the Vital and Physical Forces,' published in the "Philosophical Transactions" for 1850.

—confirmed, as they have been, by the results of many similar inquiries—seem to place it beyond doubt that the amount of Motor energy put forth is so completely out of proportion to that of the muscular tissue which we can suppose to have been consumed, that we cannot do otherwise than attribute it in great part to the oxygenization of the non-azotized components of the Blood during its passage through the muscle. What is the peculiar condition which determines this oxidation is at present undetermined; but it would seem not improbably related to the electric changes of which (as will be shown hereafter) the contracting muscle is the seat.

20. The case seems different, however, in regard to the generation of Nerve-force; for there is great reason to believe that its production is mainly, if not entirely, dependent upon the oxygenation of the Nerve-substance itself. Its rapid metamorphosis, particularly in the cortical substance of the brain, is indicated alike by many histological characters. and by the appearance of the special products of that metamorphosis in the Urine; where the quantity of the alkaline phosphates, whose production may fairly be attributed to the oxidation of the phosphorized fats of the nerve-tissue, bears a very close relation to the quantity of Brain-work executed. The enormous supply of Blood which the Brain receives,—as much as *one-fifth* part of the whole Arterial stream being sent to an organ whose weight does not exceed *one-fortieth* that of the entire body,—is another evidence of the activity of the changes continually in progress between the Blood and the Nerve-substance. We may roughly liken the Brain to a Galvanic battery, and the Blood to its exciting liquid. When the circuit is closed, a rapid oxygenation of the Nerve-substance, as of the zinc of the battery, takes place; and a corresponding equivalent of Nerve-force (which seems closely related to, but not identical with, Electricity) is generated. But the Blood also serves for the nutritive renewal of the Nerve-substance in its intervals of repose; thus supplying it with the "potential energy," which is converted into "actual energy" by the oxygenation that destroys it as a living tissue.—How intimate is the dependence of the generation of Nerve-force on the supply of Blood to the Brain, is proved by the effect of its suspension; for if this be complete, there is an immediate cessation of consciousness and motor power. And that this cessation of activity is due rather to the want of the Oxygen supplied by the Blood, than to that of its nutrient material, appears from the experiments of Professor Bert, of the Collége de France. For having, by means of an apparatus capable of including the entire human body, and of being exhausted of its air to any required degree, brought on the faintness and exhaustion—proceeding even to a state resembling asphyxia—which is known as the *mal des montagnes*, he found that this was immediately and completely relieved by the inspiration of air highly charged with oxygen. And two aëronauts, MM. Crocé-Spinelli and Sivel, having inspired from bags containing such a mixture, found themselves in possession of their consciousness and power of exertion, under a diminution of pressure which had reduced Messrs. Glaisher and Coxwell to a state of insensibility.*

21. To sum up:—The Life of Man essentially consists in the manifestation of Forces of various kinds, of which his Organism is the instrument; and these Forces are developed by the retrograde metamorphosis of the Organic Compounds generated by the instrumentality of the Plant, whereby they ultimately return to the simple binary forms (water, carbonic acid, and ammonia), which serve as the food of plants. Of these organic Compounds,

* "Comptes Rendus," March 30, 1874.

one portion (*a*) is converted into the tissues of the living body, by a constructive force which (in so far as it is not supplied by the direct agency of external Heat) is developed by the retrograde metamorphosis of another portion (*b*) of the food. And whilst the ultimate descent of the first-named portion (*a*) to the simple condition from which it was originally drawn, becomes one source of the peculiarly Animal powers—the *psychical* and the *motor*—exerted by the organism, another source of these may be found in a like metamorphosis of a further portion (*c*) of the food which has never been converted into living tissue. The generative force, as in the Plant, is evidently an expression of the ordinary constructive force; and there seems reason, moreover, for regarding it as a very high expression, its too rapid expenditure producing a peculiarly depressing effect upon the vital power of the organism, which tends to its dissolution.—But whilst we find the ultimate source of the whole vital power of the organism in the supplies of Food and of Heat which it derives from external sources, it must never be forgotten that its capacity to avail itself of those supplies depends upon its own original constitution; and that as the form into which the Germ develops itself depends upon its own *specific* endowments, so the particular modification of that form presented by each individual must depend (all external conditions being the same) upon its own *individual* endowments—the differences between these being at present only vaguely referable to antecedent conditions of the parental organism.

CHAPTER II.

DISTINCTIVE CHARACTERISTICS OF MAN.

22. In entering upon the study of that aggregation of phenomena which constitutes the Life of Man, it seems appropriate in the first instance to consider his relations to other types of Animal organization; and to examine what there is in his corporeal and psychical characters, which most distinctly differentiates him from the beings he most nearly resembles. All Zoologists are agreed that his place is at the head of the Mammalian class of the Vertebrate sub-kingdom; and that as regards both the general plan of conformation and the details of anatomical structure, there is a very close approximation between the genus *Homo* and the semi-erect tail-less Apes belonging to the genera *Troglodytes* and *Pithecus*. But there is a considerable difference of opinion as to the mode in which this relationship should be expressed. By Linnæus, the Apes and Man were included with Lemurs and Bats in one and the same Order Primates; and in this non-separation of Man from the Apes, he has been followed by several modern Zoologists of great eminence. On the other hand, Blumenbach, who in this was followed by Cuvier, maintained that the distinctive characters of the genus *Homo* are sufficient to entitle man to rank as the type of a separate Order, to which he gave the name of Bimana, considering it to be specially distinguished by the possession of two hands from the Quadrumana, which possess four nearly similar hand-like extremities. And Prof. Owen has recently gone a step further, by raising *Homo* into a sub-class Archencephala, on the ground that his "psychological powers, in association with his extraordinarily developed brain, entitle the group which he represents to equivalent rank with the

other primary divisions of the class Mammalia, founded on cerebral characters."* Although the discussion of questions of systematic arrangement is the proper business of the Zoologist, yet the inquiry into the exact nature and amount of the differences between *Man* and the (so-called) *Quadrumana* falls legitimately within the province of the Physiologist, and may therefore be appropriately dealt with in this place. In the pursuit of this inquiry, it is most important to distinguish between those structural peculiarities of which alone the Anatomist can take cognizance, and those psychical manifestations of which the sources are altogether beyond his ken; for these two orders of facts cannot be legitimately brought into the same category, and any attempts to blend them can lead to nothing but confusion. It is the province of the Comparative Anatomist to deal with Man's corporeal organism, as if he knew nothing more than the facts brought under his observation in the dissecting-room; scrutinizing every peculiarity in its structure in exactly the same spirit, and valuing it according to exactly the same measure, that he would bring to the investigation of the peculiarities of some newly-discovered type, known to him only by dead specimens. And although he might safely assign to the genus *Homo* a structural capacity for the erect posture,—a speciality in the conformation of the anterior and posterior extremities, imparting to the former a peculiar power of varied and minute prehension, and fitting the latter for biped progression,—and a relatively-larger and more complex brain, rendering it probable that the psychical faculties of which it is the instrument would be more elevated and more predominant,—yet there he must stop; since he cannot discover in Man's corporeity the faintest indication of those Intellectual and Moral attributes by which he holds himself to be specially distinguished from the brute creation, of that Progressive Reason which draws even the Infinite within its scope, of that upward aspiration after Truth and Goodness which ranges even beyond his intellectual conception, of that yearning after a purely Spiritual existence which refuses to recognise in bodily decay anything but the liberation of the imprisoned Soul. These are facts of Man's nature not less necessary to be taken into account in the estimation of his position in the Universe than those which are supplied by his bodily organization; and it is not surprising that by a too exclusive regard to them, many eminent Naturalists, from Aristotle downwards, have been led to maintain that Man ought not to be included in the Animal Kingdom at all, but should be ranked in a Kingdom by himself. This, however, is a position which cannot be consistently held by any one who recognises Anatomical structure as the true basis of Zoological classification. For granting that Man is distinguished from every other form of terrestrial being by psychical attributes which bring him into relation with Infinite Intelligence, he does not the less belong to the Animal Kingdom in his present stage of existence, in virtue of his possession of every attribute by which an Animal is characterized, and the absence of any peculiarity whatever in his organization which can be shown to remove him from that category. And since it is only *as an animal* that he is taken cognizance of by the Zoologist, it is only with his structural characters that the Zoologist should concern himself. In this point of view it appears to the author clearly demonstrable that the structural distinctions by which Man is separated from the higher Apes are much smaller in amount than those by which the latter are separated from the lower Quadrumana; and hence that the Linnæan association of *Man*

* 'On the Characters and Classification of the Mammalia,' in "Journal of the Proceedings of the Linnæan Society," vol. ii. 1857, p. 33.

and the *Quadrumana* in the same primary group is much more correct than the ordinal separation of the *Bimana* and *Quadrumana* maintained by Cuvier, and *à fortiori* than the proposition of Prof. Owen to rank Man in a distinct sub-class.

23. As the ordinal separation of the *Bimana* from the *Quadrumana* has come to be generally accepted upon the authority of Cuvier, it will be desirable to begin by examining into the validity of the characters on which it rests; comparing, in the first place, the hand and the foot of Man with the corresponding extremities of the higher Apes; and then inquiring whether the differences which they respectively present, either surpass in *degree* those with which we meet in a like comparison between the extremities of the higher Apes and those of the lower Monkeys, or can be justly held to depart from them in *kind*. There is in Man, what we observe in none of the Mammalia which approach him in other respects, a complete distinction in the character of the anterior and posterior extremities; the former being adapted for prehension alone, and the latter almost exclusively for support and progression: and thus each function is performed with much greater completeness, than it can be when two such opposite purposes have to be united. "That," says Cuvier, "which constitutes the *hand*, properly so called, is the faculty of opposing the thumb to the other fingers, so as to seize upon the most minute objects; a faculty which is carried to its highest degree of perfection in Man, in whom the whole anterior extremity is free, and can be employed in pre-

Fig. 1.

Hand of *Man*, compared with anterior extremity of *Orang*.

hension." The peculiar prehensile power possessed by the *Hand* of Man is chiefly dependent upon the size and power of the thumb; which is more developed in him, than it is in the highest Apes (Fig. 1). The thumb of the Human hand can be brought into exact opposition to the extremities of all the fingers, whether singly or in combination; while in those Quadrumana which most nearly approach Man, the thumb is so short, and the fingers so much elongated, that their tips can scarcely be brought into opposition; and the thumb and fingers are so weak, that they can never be opposed to each other with any degree of force. Hence, although well suited to cling round bodies of a certain size, such as the small branches of trees, &c., the anterior extremities of the Quadrumana can neither seize very minute objects with such precision, nor support large ones with such firmness, as are essential to

the dexterous performance of a variety of operations for which the hand of Man is admirably adapted. This adaptation, however, is not obtained by means of any new instrumentality; for the anterior extremity of the Orang or Chimpanzee possesses not only every bone, but every muscle, which is found in that of Man; and its only structural differences consist in the proportionate development of the several components of these organs respectively.—But the functional powers of the anterior extremity are not related solely to its own structure; since the use that can be made of the limb depends in part upon its relations to the body at large, the general conformation of which must be adapted to turn its special capacity to advantageous account. Thus, while the arm of the higher Apes has as wide a range of motion as that of Man, so far as its articulation is concerned, it is only when the animal is in the erect attitude that the limb can have free play. And even the most perfect organization of the hand as an instrumental structure would be comparatively valueless, without the *mind* by which its actions are prompted, and the *senses* by which they are guided.

24. The *Foot* of Man, in like manner, differs from that of the higher Apes, in those characters which specially adapt it to the support of the body in the erect posture, and to biped progression; in which adaptation it loses much of that prehensile power which the posterior extremities of the higher Quadrumana possess almost equally with their anterior. The Human foot is, in proportion to the size of the whole body, larger, broader, and stronger, than that of any other Mammal save the Kangaroo. The surface of the Astragalus, which articulates with the tibia, looks almost vertically upwards, and hardly at all inwards when the sole is flat upon the ground, and the lateral facets are more nearly at right angles to this surface than in any Ape. The plane of the foot is directed at right angles to that of the leg; and its sole is concave, so that the weight of the body falls on the summit of an arch, of which the os calcis and the metatarsal bones form the two points of support. This arched form of the foot, and the contact of the whole plantar surface with the ground,

Fig. 2.

Foot of *Man*, compared with posterior extremity of *Orang*.

are peculiarly noticeable in Man; most of the Apes having the os calcis small, straight, and more or less raised from the ground, which they touch, when standing erect, with the outer side only of the foot (Fig. 2). The function of the *hallux*, or great-toe, moreover, is strikingly contrasted in Man and the

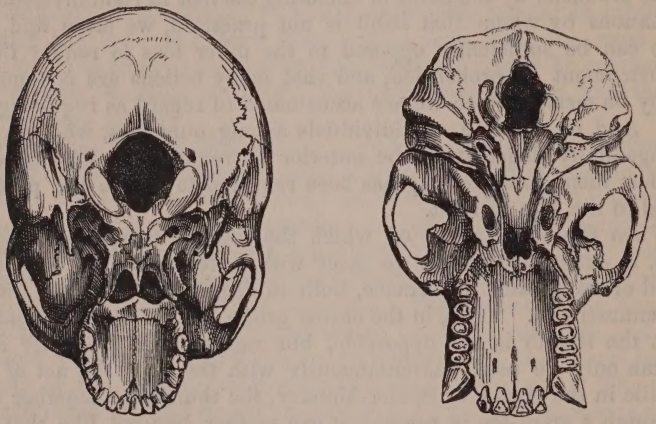
Apes; for whilst in the latter it is nearly as opposable as the thumb, and can be used to almost the same degree as an instrument of prehension, it chiefly serves in the former to extend the basis of support, and to advance the body in progression. But neither in its osteology nor in its myology is there any essential difference between the foot of Man and the posterior extremity of the higher Apes; for every bone and every muscle in the one has its counterpart in the other; and there is nothing which really assimilates the posterior to the anterior extremity of the Ape, or entitles the former to be considered as a hand, save the opposability of the great-toe. It is certain, moreover, that this faculty is not originally wanting in Man, although it may be destroyed by the disuse produced by the habit of enclosing the foot in rigid investments; for among nations by whom that habit is not practised, we often find that the great-toe can be sufficiently opposed to the other toes to render the foot a useful instrument of prehension, and that many actions are commonly performed by its means, which we are accustomed to regard as requiring *manual* agency. And in the case of individuals among ourselves, who have either been congenitally deficient in the anterior extremities, or who have subsequently lost them, practice only has been required to enable the posterior to be turned to the like account.

25. When the comparison, of which the leading points have now been sketched, is extended further, we meet with differences that cannot but be accounted of far greater importance, both in degree and in kind, than those already enumerated. Thus, in the entire group of *Platyrrhine* Monkeys, we find that the thumb is not opposable, but ranges with the other digits, so that it can only be used consentaneously with them in the act of prehension; while in the *Ateles*, or Spider-Monkey, the thumb is altogether wanting, and although a great-toe is present, it can neither be used like that of Man for support, nor be opposed to the other digits as in the higher Quadrumana, the posterior and anterior extremities being strikingly assimilated in structure, and being alike adapted to serve only as *claspers*. Among the Baboons and Lemurs, moreover, we find that the conformation alike of the anterior and of the posterior extremities is such as to assimilate them at least as much to the lower *quadrupedal* as to the higher *quadrumanous* type; so that between the two extremes of the series of which the anthropoid Apes are the highest and the Baboons and Lemurs are the lowest members, there is a far wider interval, as regards the conformation of the extremities, than that which separates the former from Man.

26. The next series of distinctive characters to be considered, are those by which Man is adapted to the erect attitude.—On examining his *Cranium*, we remark that the occipital condyles are so placed, that a perpendicular dropped from the centre of gravity of the head would nearly fall between them, so as to be within the base on which it rests upon the spinal column. The foramen magnum is not placed in the centre of the base of the skull, but just behind it; so that the greater specific gravity of the posterior part of the head, which is entirely filled with solid matter, is compensated by the greater length of the anterior part, which contains many cavities. There is, indeed, a little over-compensation, which gives a slight preponderance to the front of the head, so that it drops forwards and downwards when all the muscles are relaxed; but the muscles attached to the back of the head are far larger and more numerous than those in front of the condyles, so that they are evidently intended to counteract this disposition; and we accordingly find ourselves able to keep up the head for the whole day with so slight and involuntary an effort that no fatigue is produced by it. Moreover, the

plane of the foramen magnum and the surfaces of the condyles have a nearly horizontal direction when the head is upright; and thus the weight of the skull is laid vertically upon the top of the vertebral column.—If these arrangements be compared with those which prevail in other Mammalia, it will be found that the foramen and condyles are placed in the latter much nearer the back of the head, and that their plane is more oblique. Thus, whilst the foramen magnum is situated in Man just behind the centre of the base of the skull, it is found in the Chimpanzee and Orang Outan to occupy the middle of the posterior third (Fig. 3); and, as we descend through the scale of

Fig. 3.



View of the base of the Skull of *Man*, compared with that of the *Orang Outan*.

Mammalia, we observe that it gradually approaches the *back* of the skull, and at last comes nearly into the line of its longest diameter, as we see in the Horse. Again, in all Mammalia except Man, the plane of the condyles is oblique, so that, even if the head were equally balanced upon them, the force of gravity would tend to carry it forwards and downwards; in Man, the angle which they make with the horizon is very small; in the Orang Outan, it is as much as 37°; and in the Horse, their plane is vertical, making the angle 90°. If, therefore, the natural posture of man were horizontal, the plane of his condyles would be brought, like that of the Horse, into the vertical position; and the head, instead of being nearly balanced on the summit of the vertebral column, would hang at the end of the neck, so that its whole weight would have to be supported by some external and constantly-acting power. But for this, there is neither in the skeleton, the ligamentous apparatus, nor the muscular system of Man, any adequate provision; so that in any other than the vertical position, his head, which is relatively heavier than that of most Mammalia, would be supported with more difficulty and effort than it is in any other animal.

27. The position of the *Face* immediately beneath the brain, so that its front is nearly in the same plane as the forehead, is peculiarly characteristic of Man; for in the skulls of the Chimpanzee and Orang, which approach nearest to that of man, the cranial portions are rather posterior to, than above, the facial (Figs. 4, 7). The projection of the muzzle, taken in connexion with the obliquity of the condyles, is another evidence of want of perfect adaptation to the erect posture; whilst the absence of prominence in the face of Man shows that none but the erect position can be natural to him. For supposing

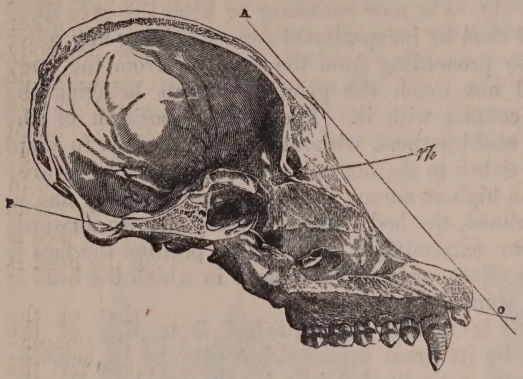
that, with a head formed and situated as at present, he were to move on all-fours, his face would be brought into a plane parallel with the ground; so that as painful an effort would be required to examine with the eyes an object placed in front of the body, as is now necessary to keep the eyes fixed on the zenith; the nose would then be incapacitated from receiving any other odorous emanations than those proceeding from the earth or from the body itself; and the mouth could not touch the ground without bringing the forehead and chin also into contact with it. The oblique position of the condyles in the Quadrumana enables them, without much difficulty, to adapt the inclination of their heads either to the horizontal or to the erect posture; but the natural position, in the highest among them, is unquestionably one in which the spinal column is inclined, the body being partially thrown forwards so as to rest upon the anterior extremities; and in this position the face is directed forwards without any effort, owing to the mode in which the head is obliquely articulated with the spine (Fig. 7).

28. The Cranium of Man is further distinguished from that of the anthropoid Apes, not merely by its great capacity, but also by its smoothness; its surface being almost entirely deficient in those ridges for the attachment of muscles, which are remarkably strong in both the Chimpanzee and the Orang, and which impart to its configuration somewhat of a carnivorous aspect. This aspect is strengthened by the great depth of the temporal fossa, and by the extent and strength of the zygomatic arch; features that are most remarkably developed in the *Troglodytes gorilla* (Fig. 7). The breadth of the upper part of the face is a noticeable feature in Man; the eyes being set widely apart, and the interorbital space occupying one-fourth of the interval between the outer walls of the orbits.* The inner walls of the orbits formed by the ossa plana of the ethmoid are nearly parallel to one another. Moreover, the jaws in even the most degraded races of Man project far less from the general plane of the face than they do in the Apes; and his teeth are arranged in a continuous series, without any hiatus or any considerable difference in length; whilst all the Apes, in their adult state at least, are furnished with canine teeth of extraordinary length, between the sockets of which and those of the adjoining teeth (anteriorly in the upper jaw, and posteriorly in the lower) there is a vacant space or 'diastema.' Even in the most prognathous Human skulls, moreover, the incisors meet each other much more nearly in the same axis than they do in the anthropoid Apes, in which they form an angle with each other that is not nearly so divergent. The fusion of the intermaxillary or premaxillary bones with the superior maxillary, at an early period of fœtal life, is a remarkable character of the Human cranium, as distinguishing it from that of the Apes, in which the intermaxillary bones remain separate to a much later period, sometimes differing also very considerably both in size and shape. Thus, in the *Troglodytes gorilla*, these bones are not only remarkable for their prominence, but also for their upward extension round the nostrils, so that they completely exclude the maxillary bones from their borders, and from the basis of support for the nasal bones; and although they coalesce with the maxillaries at and near the alveolar portion, they remain separate elsewhere. The lower jaw of Man is remarkable for that prominence at its symphysis which forms the chin; and although this, also, is least developed in the most prognathous Human crania, yet it is never so deficient as it is in the lower jaw of the Chimpanzee and

* Huxley's "Anatomy of the Vertebrate Animals," 1871, p. 489.

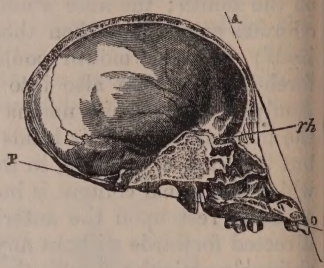
Orang.—It is curious to observe that the skulls of the *young* of Man and of the anthropoid Apes resemble one another much more than do those of the

Fig. 4.



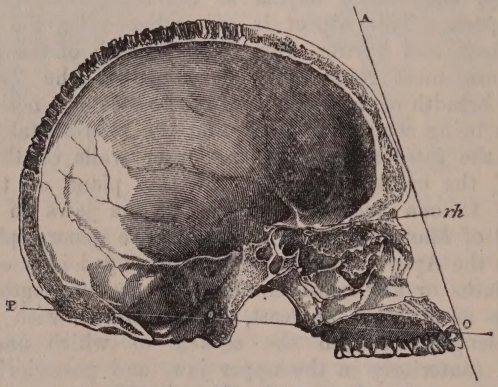
Vertical section of Skull of *Adult Orang.*

Fig. 5.



Vertical section of Skull of *Young Orang.*

Fig. 6.



Vertical section of Skull of *Papuan Negrito.*

adults; each tending to diverge, in its advance towards full development, from a type which seemed almost similar in both (Figs. 4, 5, 6). It is at the time of the second dentition that the muzzle of the anthropoid Apes acquires its peculiar elongation and consequent projection in front of the forehead (Figs. 5, 4); and the whole cast of the features is altered at the same time, so that it approaches much more to that of the lower Quadrumana than would be supposed from observation of the young animal only.* In the Human subject, on the other hand, we see that, although in the advance from childhood to adult age, there is a progressive enlargement of the face in proportion to the capacity of the cranial cavity, this augmentation is comparatively small in amount, and but little affects the general configuration of the cranium.†

29. The great size of the *cranial* portion of the skull in Man, as compared

* None but young specimens of the Chimpanzee and Orang Outan have ever been brought alive to this country; and they have never long survived the period of their second dentition.

† See Prof. Owen's Papers on the Anatomy of the Orang and Chimpanzee, in the "Zoological Transactions," vols. i. and iii.; and Prof. Vrolik in the Art. *Quadrumana* in the "Cyclopædia of Anatomy and Physiology," vol. iv.

with the *facial*, produces a marked difference between his 'facial angle' and that of even the highest Quadrumana. According to Camper, who first applied this method of measurement, the 'facial angle' of the average of European skulls is 80°, whilst in the ideal heads of the Grecian gods it is increased to 90°; on the other hand, in the skull of a Kalmuck he found it to be 75°, and in that of a Negro only 70°; and applying the same system of measurement to the skulls of Apes he found them to range from 64° to 60°. But these last measurements were all taken from young skulls, in which the forward extension of the jaws, which takes place on the second dentition, had not yet occurred. In the adult Chimpanzee, as Prof. Owen has shown, the 'facial angle' (Figs. 4, 5, 6, A O P) is no more than 35°, and in the adult Orang only 30°; so that instead of the Negro being nearer to the Ape than to the European, as Camper's estimate would make him, the interval between the most degraded Human races and the most elevated Quadrumana is considerably greater than between the highest and the lowest forms of Humanity. It must be borne in mind, however, that the 'facial angle' is so much affected by the degree of prominence of the jaws that it can never afford any certain information concerning the elevation of the forehead and the capacity of the cranium; all that it can in any degree serve to indicate, being the relative proportion between the facial and the cranial parts of the skull. This proportion is far more correctly determined, as Prof. Owen has shown,* by vertical sections of the skulls to be compared, through their median planes (Figs. 4, 5, 6); and from an extended comparison of such sections, it appears that whilst the difference between the cranial cavity of the higher Apes and that of Man is rather one of relative size than of conformation, there is a far more strongly-marked difference, not only in relative size but also in conformation, between the cranial cavities of the higher and those of the lower Quadrumana, the latter being not only far less capacious in proportion to the size of the body, but being also disposed in such a manner that its long diameter comes to be continuous (as in Quadrupeds generally) with the axis of the spinal canal, instead of crossing it nearly at right angles as in Man. The length of the cerebral cavity in Man is more than twice that of the basi-cranial axis. Its capacity in the healthy adult is invariably more than forty cubic inches, and may rise to more than a hundred cubic inches (Huxley).

30. The *Vertebral Column* in Man, although not absolutely straight, has its curves so arranged that, when the body is in an erect posture, a vertical line from its summit would fall exactly on the centre of its base. It increases considerably in size in the lumbar region, so as altogether to be somewhat pyramidal in form. The lumbar portion in the Chimpanzee and Orang is not of the same proportional strength, and contains but four vertebræ instead of five. The processes for the attachment of the dorso-spinal muscles to this part are peculiarly large and strong in Man; and this arrangement is obviously adapted to overcome the tendency which the weight of the viscera in front of the column would have to draw it forwards and downwards. On the other hand, the spinous processes of the cervical and dorsal vertebræ, which in other Mammalia are large and strong for the attachment of the ligaments and muscles that support the head, and which are peculiarly pronounced in the Gorilla (Fig. 7), have comparatively little prominence in Man, his head being nearly balanced on the top of the column.—The base of the Human vertebral column is

* "Zoological Transactions," vol. iv. p. 77 *et seq.*

placed on a sacrum of greater proportional breadth than that of any other animal; this sacrum is fixed between two widely-expanded ilia; and the whole *pelvis* is thus peculiarly broad. In this manner, the femoral articulations are thrown very far apart, so as to give a wide basis of support; and by the oblique direction of the pelvis, the weight of the body is transmitted almost vertically from the top of the sacrum to the upper part of the thigh bones. The pelvis of the anthropoid Apes is very differently constructed; as will be seen in the adjoining PLATE, in which the skeleton of the Orang is placed in proximity with that of Man. It is much larger and narrower; its alæ extend upwards rather than outwards, so that the space between the lowest ribs and the crest of the iliac bones is much less than in Man; their surfaces are nearly parallel to that of the sacrum, which is itself longer and narrower; and the axis of the pelvis is nearly parallel with that of the vertebral column. The position of the Human femur in which its head is most securely retained in its deep acetabulum is that which it has when supporting the body in the erect attitude; in the Chimpanzee and Orang its analogous position is at an oblique angle to the long axis of the pelvis, so that the body leans forwards in front of it (Fig. 7); in many Mammalia, as in the Elephant, it forms nearly a right angle with the vertebral column; and in several others, as the Horse, Ox, &c., the angle which it makes with the axis of the pelvis and vertebral column is acute. In these respects, then, the skeleton of Man presents an adaptation to the erect posture, which is exhibited by that of no other Mammal; but that of the anthropoid Apes presents a far nearer approximation to the Human model in all the foregoing particulars, than it does to that of the lower Quadrumana.

31. There is a considerable difference in the form of the *trunk* between Man and most other Mammalia; for his thorax is expanded laterally, and flattened in front, so as to prevent the centre of gravity from being carried too far forwards; and his sternum is short and broad. Between the bony walls of the thorax and the margin of the pelvis a considerable space intervenes, which is occupied solely by muscles and tegumentary membranes; and these would be quite insufficient to sustain the weight of the viscera, if the habitual position of the trunk had been horizontal.—In these particulars, however, the most anthropoid Apes agree more or less completely with Man.

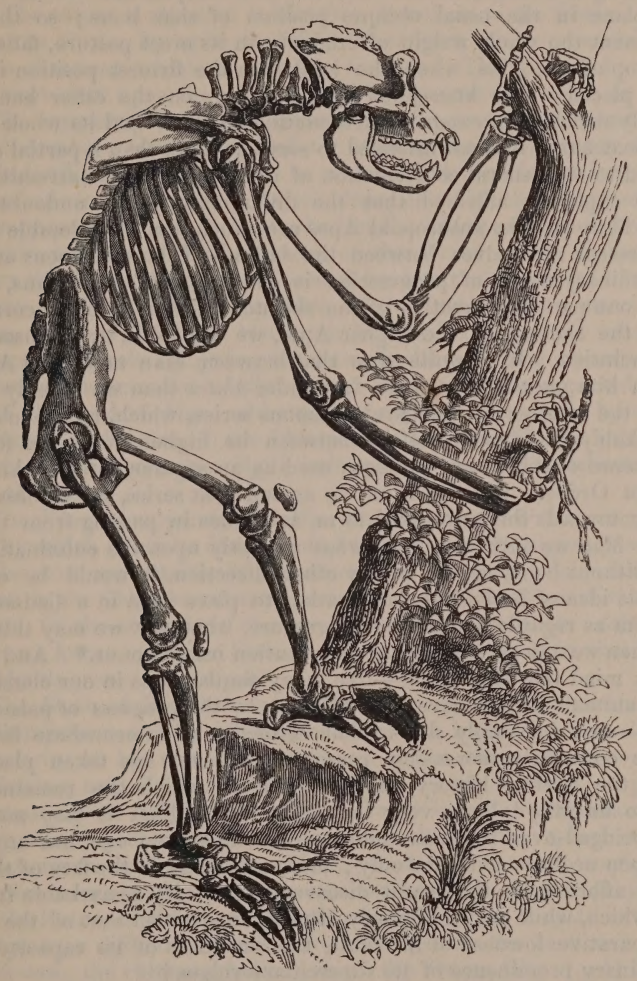
32. The *lower extremities* of Man are remarkable for their relative length, which is greater than that which we find in any other Mammalia, except the Kangaroo tribe. The chief difference in their proportions between Man and the semi-erect Apes is seen in the thigh; and it is from the relative length of this part in him that the middle point of the height of the body is in the adult as low as the symphysis pubis, and further from the comparative shortness of his anterior extremities, his hands only reach the middle of his thighs, whilst in the Chimpanzee they hang on a level with the knees (Fig. 7), and in the Orang they descend to the ankles (PLATE).* The Human femur is

* The following Table (Beaunis, "Nouveaux Éléments de Physiologie Humain," p. 40) gives the lengths of the limbs as compared with the vertebral column in Man and the higher Apes:—

	European.	Bushman.	Gorilla.	Chimpanzee.	Orang.
Vertebral column	100	100	100	100	100
Arm	80	78	115	96	122
Leg	117	110	96	90	89
Hand	26	26	36	43	48
Foot	35	32	41	39	52

distinguished, however, by its form and position, as well as by its length. The obliquity and length of its neck still further increase the breadth of the

Fig. 7.



Skeleton of *Troglodytes Gorilla.*

hips; whilst they cause the lower extremities of the femora to be somewhat obliquely directed towards each other, so that the knees are brought more into the line of the axis of the body. This arrangement is obviously of great use in facilitating the purely *biped* progression of Man, in which the entire weight of the body has to be alternately supported on each limb; for if the knees had been kept further apart, the whole body must have been swung from side to side at each step, so as to bring the centre of gravity over the top of each tibia; as is seen to a certain extent in the female sex, whose walk, owing to the greater breadth of the pelvis and the separation between the knees, is less steady than that of the male. There is also a marked difference

between the knee-joint of Man and that of even the highest Apes. In the former, the opposed extremities of the femur and the tibia are so expanded as to present a very broad articulating surface, and the internal condyle of the femur being the longer of the two, the two condyles are in the same horizontal plane in the usual oblique position of that bone; so that by this arrangement the whole weight of the body, in its erect posture, falls vertically on the top of the tibia, when the joint is in the firmest position in which it can be placed. The knee-joint of the Orang, on the other hand, is comparatively deficient in extent of articulating surface; and its whole conformation indicates that it is not intended to serve as more than a partial support.—In regard to the general conformation of the bones of the extremities, it may be most explicitly affirmed that the differences which undoubtedly exist between Man and the anthropoid Apes are much less considerable than those which present themselves between the latter and those Baboons and Lemurs whose ordinary mode of progression is *quadrupedal*. And thus, after contrasting one part after another of the skeleton of Man with the corresponding parts of the skeleton of the higher Apes, we are led in every instance to the same conclusion. It is quite true that between Man and those Apes which approach him most closely there is a wider *hiatus* than we usually meet with between the members of the Quadrumanous series, which, as a whole, presents a remarkably gradational position between its higher and lower forms; and the existence of this *hiatus* has been used as an argument for ranking Man in a distinct Order. But since, as we ascend that series, we witness a gradual tendency towards the anthropoid form, and since in passing from the highest Apes to Man we only come somewhat abruptly upon the culmination of that ascent without being led off in any other direction, it would be contrary to the whole idea of Zoological classification to place Man in a distinct category from them as regards his corporeal structure, whatever we may think it right to do when we take his psychical constitution into account.* And it is to be borne in mind that this *hiatus*—like many similar gaps in our classification of existing animals which have been filled up by the progress of palæontological research—*may* be simply due to that extinction of intermediate forms which (there is constantly increasing reason to believe) has taken place in past ages of the Earth's history, to an extent of which the remains hitherto known to us afford but a very imperfect idea. That it *may not* be completely bridged-over by such intermediate links, no one has any right to affirm upon negative evidence only; more especially in the face of the positive evidence afforded by the recent discovery of a very remarkable fragment of a skull which, while unquestionably Human, resembled that of the Gorilla in the comparative lowness of its vault, the smallness of its capacity, and the extraordinary prominence of its superciliary ridges.†

33. The most characteristic peculiarity of the Human *Myology* is the great

* We meet with a similarly abrupt transition at the other extremity of the series, in the *Cheiromys* or Aye-aye; an animal which Zoologists now agree to rank among the Quadrumana in virtue of its general Lemurine affinities, although in dentition and several other particulars it bears so strong a resemblance to the Rodents as to have been placed among them by Cuvier.

† See "Nat. Hist. Rev.," vol. i. 1861, p. 155; and Prof. Huxley 'On some Fossil Remains of Man,' in his "Evidence as to Man's Place in Nature," 1863. The anatomical peculiarities of Man are very completely given by Prof. Huxley, in his "Anatomy of Vertebrated Animals," 1871, p. 488 *et seq.;* see also Broca, "L'ordre de Primates Bulletin de la Soc. d'Anthropol.," 1869. The student will find an admirable exposition of the structural resemblances and differences between Man and Apes in St. George Mivart's little work, entitled "Man and Apes," 1873. In this work Mr. Mivart strongly opposes the doctrine of the descent of Man and Apes from a common ancestor.

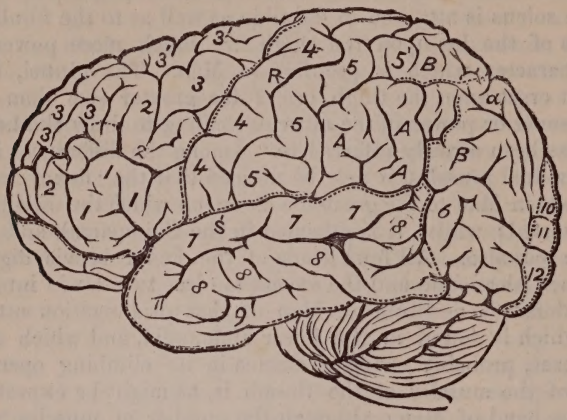
development of those muscles of the trunk and limbs which contribute to the maintenance of the erect posture. Thus, the gastrocnemii, and the other muscles which tend to keep the leg erect upon the foot, form a much more prominent 'calf' than is seen either in the most anthropoid Apes, or in any other animal. The soleus is attached to the tibia as well as to the fibula. So, again, the extensors of the leg upon the thigh are much more powerful than the flexors; a character which is peculiar to Man. The glutæi, by which the pelvis is kept erect upon the thigh, are of far greater size than is elsewhere seen. The superior power of the muscles tending to draw the head and spine backwards has been already referred-to. Among the differences in the attachment of individual muscles, it may be noticed that the 'flexor longus pollicis pedis' proceeds in Man to the great-toe alone, on which the weight of the body is often supported; whilst it is attached in the Chimpanzee and Orang to the three middle toes also. All four heads of the flexor brevis digitorum pedis arise from the Calcaneum, and the second toe has two dorsal interossei. The 'latissimus dorsi' is destitute in Man of that prolongation attached to the olecranon, which is found in the lower Mammalia, and which exists even in the Chimpanzee, probably giving assistance in its climbing operations. The larger size of the muscles of the thumb is, as might be expected, a characteristic of the hand of Man; although the number of muscles by which that digit is moved is the same in the Chimpanzee as in the Human subject. The separation of the 'extensor digiti indicis,' however, as a distinct muscle, is peculiar to Man.

34. The *Visceral* apparatus of Man presents very few characteristic peculiarities by which it can be distinguished from that of the higher Quadrumana; among the most remarkable is the absence of the laryngeal pouches, which exist even in the Chimpanzee and Orang Outan, as dilatations of the laryngeal ventricles. Of the anatomy of the last-named animals in their *adult* condition, however, we know as yet too little to enable its conformity to that of Man to be confidently pronounced upon.

35. The *Brain* of Man does not differ so much in conformation from that of the Chimpanzee, and in this respect still more highly-developed Orang, as the superiority of his mental endowments might have led us to anticipate. The following are the principal differences which it seems to present:—1. The mass of the entire brain is considerably larger in proportion to that of the body, and in proportion also to the diameter of the spinal cord, and of the nerves which are connected with it.—2. In the external configuration of the Cerebrum we notice that its *anterior* lobes are larger, project further beyond the Rhinencephalon, or Olfactive Ganglion, than they do in the highest Quadrumana; a difference which is well marked in the sectional contour of the brain-case, the rhinencephalic fossa of the Orang (Fig. 4, *rh*) being at its most anterior part; whilst even in the least elevated forms of the Human skull, this fossa (of which the cribriform plate of the ethmoid bone constitutes the floor) has no inconsiderable part of the cranial cavity in front of it (Fig. 6, *rh*). —3. The Cerebrum as a whole projects further beyond the Cerebellum than in the Quadrumana generally, which is due, not to any increase in size of the occipital Convolutions, but to the great development of the 'bridging convolutions' interposed between the parietal and occipital lobes.—4. The Convolutions are more numerous and complex, and usually more or less unsymmetrical, and the sulci are deeper. It appears, however, that in the lower races of Mankind the brain presents, both in the simplicity and the precise symmetry of its convolutions, a much closer approximation to the Quadrumanous type than it does in the higher.—5. On examining the internal struc-

ture it is found that the peripheral layer of grey matter is thicker, the corpus callosum extends further backwards, and the posterior cornua of the lateral

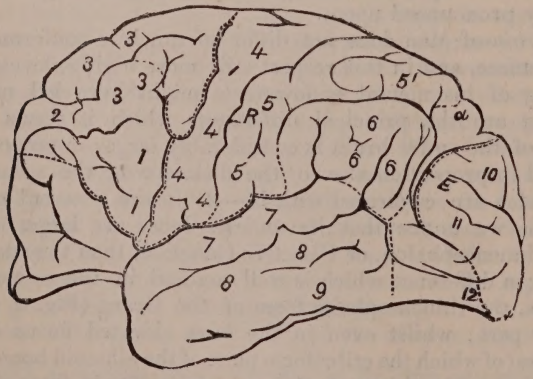
Fig. 8.



Brain of Man. [The same lettering applies to all the four figures.]
1, 2, 3, Frontal convolutions. 4, 5, 6, A & B, Parietal convolutions.
7, 8, 9, Temporo-sphenoidal convolutions. 10, 11, 12, Occipital convolutions.
A is the supra-marginal lobule; B is the postero-parietal lobule; and β is on the bridging or annectent convolutions; R, fissure of Rolando; E, parieto-occipital fissure.

ventricles are relatively longer and larger than they usually are in Quadrumana.*—6. The Cerebellum, also, is proportionally larger. The relative

Fig. 9.

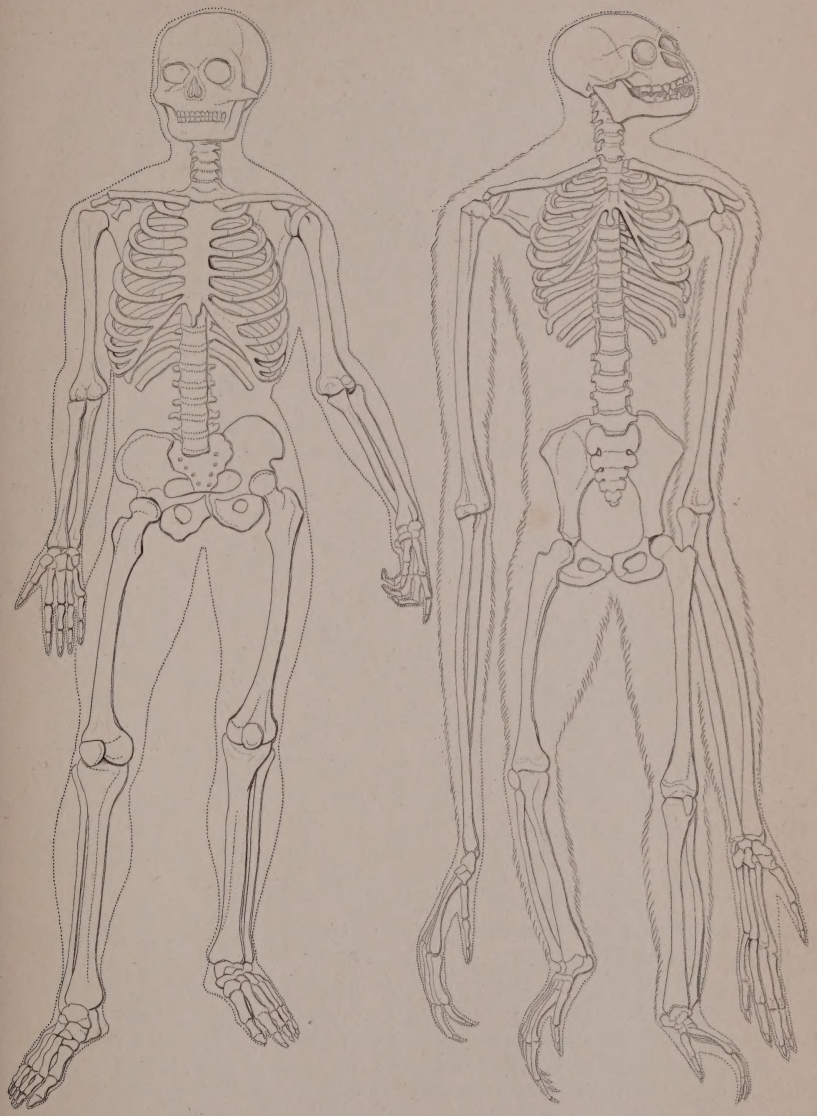


Brain of Orang (Simia). Left side.

development of the Cerebrum in Man and the three highest Apes is well shown in the accompanying drawings (Figs. 8, 9, 10).

36. The small size of the face of Man, compared with that of the cranium, is an indication that in him the *senses* are subordinate to the *intelligence*. Accordingly, we find that while he is surpassed by many of the lower animals in acuteness of sensibility to light, sound, &c., he stands pre-eminent in the

* For an excellent description of the Convolutions of the Human Cerebrum, see W. Turner "Edinb. Med. Journ.," June, 1866, and Ecker.



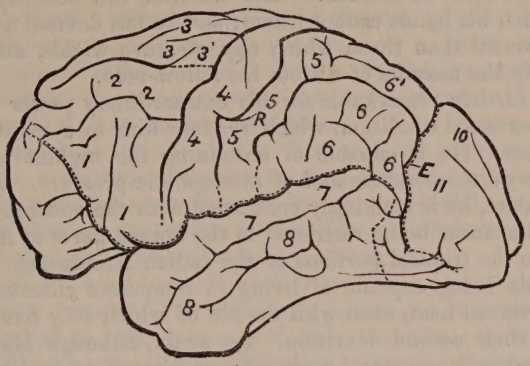
H.Adlard &c.

COMPARATIVE VIEW OF THE SKELETON OF MAN,

AND THAT OF THE OURAN OUTAN.

power of comparing and judging of his sensations, and of thence drawing conclusions as to their objective sources. Moreover, although none of his senses are very acute in his natural state, they are all moderately so; and

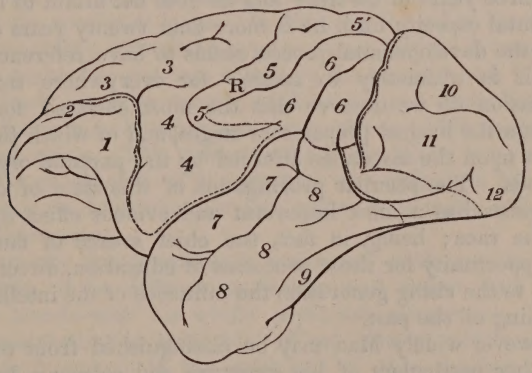
Fig. 10.



Brain of Chimpanzee (Troglodytes). Left side.

they are capable of being wonderfully improved by practice, when circumstances strongly call for their exercise. This seems especially the case with

Fig. 11.



Brain of Mandrill Baboon (Cynocephalus). Left side.

the *tactile* sense, of which Man can make greater use than any other animal, in consequence of the entire freedom of his anterior extremities; although there are many which surpass him in their power of appreciating certain classes of tactile impressions.—So, again, Man's nervo-muscular power is inferior to that of most other animals of his size: the full-grown Orang, for example, surpasses him both in strength and agility; and the Gorilla, according to the statements of the Negroes who have encountered it, is more than a match for any single man, and is almost certain to destroy any human opponent once within his grasp.—The absence of any natural weapons of offence, and of direct means of defence, are remarkable characteristics of Man, and distinguish him not only from the lower Mammalia, but also from the most anthropoid Apes; in which it is obvious (both from their habits and general organization) that the enormous canines have no relation to a carnivorous regimen, but are instruments of warfare. On those animals to

which Nature has denied weapons of attack, she has bestowed special means either of passive defence, of concealment, or of flight; in each of which Man is relatively deficient. Yet by the superiority of his reason he has been enabled not only to resist the attacks of other animals, but even to bring them into subjection to himself. His intellect can scarcely suggest the mechanism which his hands cannot frame; and he has devised and constructed arms more powerful than those which any creature wields, and defences so secure as to defy the assaults of all but his fellow-men.

37. Man is further remarkable for his extraordinary power of adaptation to varieties in external condition, which renders him to a great extent independent of them. He is capable of sustaining the highest as well as the lowest extremes of temperature and of atmospheric pressure. In the former of these particulars, he is strikingly contrasted with the anthropoid Apes; the Gorilla and Chimpanzee being restricted to the hottest parts of Africa, and the Orang Outan to the tropical portions of the Indian Archipelago; and neither of these animals being capable of living in temperate climates without the assistance of artificial heat, even with the aid of which they have not hitherto long survived their second dentition. So, again, although Man's diet seems naturally of a mixed character, he can support himself in health and strength either on an exclusively vegetable diet or an almost exclusively animal regimen.

38. The slow growth of Man, and the length of time during which he remains in a state of dependence, are peculiarities that remarkably distinguish him from all other animals. He is unable to obtain his own food during at least the first three years of his life; and he does not attain to his full bodily stature and mental capacity until he is more than twenty years of age. This retardation of the developmental process seems to have reference to the high grade which it is ultimately to attain; for everywhere throughout the Organized Creation do we observe that the most elevated forms are those which go through the longest preparatory stages, and of which the evolution is most dependent upon the assistance afforded by the parental organism during its earlier periods. The peculiar prolongation of this state of dependence in the Human species has a most important and evident effect upon the social condition of the race; being, in fact, the chief source of family ties, and affording the opportunity for those processes of education, direct and indirect, which transmit to the rising generation the influence of the intellectual culture and moral training of the past.

39. Still, however widely Man may be distinguished from other animals, by these and other particulars of his structure and economy, he is yet more distinguished by those *mental* endowments, and by the habitudes of life and action thence resulting, which must be regarded as the essential characteristics of Humanity. It is in adapting himself to the conditions of his existence, in providing himself with food, shelter, weapons of attack and defence, &c., that Man's intellectual powers are first called into active operation; but when thus aroused, their development has no assignable limit. The Will, guided by the intelligence, and acted-on by the desires and emotions, takes the place in Man of the Instinctive propensities which are usually the immediate springs of action in the lower animals; for although, among the most elevated of these, a high amount of Intelligence is exhibited, yet its operations seem to be always directly attributable to external suggestions, present or remembered; and the character never rises beyond that of the child. In fact, the correspondence between the psychical endowments of the Chimpanzee, and those of a Child of three years old who has not yet begun to speak, is very close.—One of the most important aids in the use and development of the Human

mind is the capacity for *articulate speech;* of which, so far as we know, Man is the only animal in possession. There is no doubt that many other species have certain powers of communication between individuals; but these are probably very limited, and of a kind more allied to "the language of signs" than to a proper verbal language. In fact, it is obvious that the use of a language composed of a certain number of distinct sounds, combined into words in a multitude of different modes, requires a power of intellectual abstraction and generalization, in which it appears that the lower animals are altogether deficient. So, again, verbal language affords the only means whereby abstract ideas can be communicated; and those who have perused the interesting narrative given by Dr. Howe of his successful training of Laura Bridgeman, will remember how marked was the improvement in her mental condition, from the time when she first apprehended the fact that she could give such distinct expression to her thoughts, feelings, and desires, as should secure their being comprehended by others.

40. The *capacity for intellectual progress* is a most remarkable peculiarity of Man's psychical nature. The instinctive habits of the lower Animals are limited, are peculiar to each species, and have immediate reference to their bodily wants. Where a particular adaptation of means to ends, of actions to circumstances, is made by an individual, the rest do not seem to profit by that experience; so that, although the instincts of particular animals may be modified by the training of Man, or by the education of circumstances, so as to show themselves after a few generations under new forms, no elevation of intelligence appears ever to take place spontaneously, no psychical improvement is manifested in the species at large. In Man, on the other hand, we observe not merely the capability of profiting by experience, but the determination to do so; which he is enabled to put into action by the power which his Will (when properly disciplined) comes to possess, of directing and controlling his current of thought, by fixing his attention upon any subject which he desires to keep before his mental vision. This power, so far as we know, is peculiar to Man: and the presence or absence of it constitute the difference between a being possessed of power to determine his own course of thought and action, and a mere thinking automaton.

41. Man's capacity for progress is connected with another element in his nature, which it is difficult to isolate and define, but which interpenetrates and blends-with his whole psychical character. "The Soul," it has been remarked, "is that side of our nature which is in relation with the Infinite;" and it is the existence of this relation, in whatever way we may describe it, which seems to constitute one of the most distinctive peculiarities of Man. It is in the desire for an improvement in his condition, occasioned by an aspiration after something nobler and purer, that the main-spring of human progress may be said to lie; among the lowest races of mankind, the capacity exists, but the desire seems dormant. When once thoroughly awakened, however, it seems to "grow by what it feeds on;" and the advance once commenced, little external stimulus is needed; for the desire increases at least as fast as the capacity. In the higher grades of mental development there is a continual looking-upwards, not (as in the lower) towards a more elevated Human standard, but at once to something beyond and above Man and Material Nature. This seems the chief source of the tendency to believe in some unseen existence; which may take various forms, but which seems never entirely absent from any race or nation, although, like other innate tendencies, it may be deficient in individuals. Attempts have been made by some travellers to prove that particular nations

are destitute of it; but such assertions have been based only upon a limited acquaintance with their habits of thought, and with their outward observances; for there are probably none who do not possess the idea of some invisible Power, external to themselves, whose favour they seek, and whose anger they deprecate, by sacrifice and other ceremonials. It requires a higher mental cultivation than is commonly met-with, to conceive of this power as having a spiritual existence; but wherever the idea of Spirituality can be defined, this seems connected with it. The vulgar readiness to believe in ghosts, demons, &c., and the vagaries of the so-called 'Spiritualists' of recent times, are only irregular, or depraved manifestations of the same tendency. Closely connected with it is the desire to participate in this spiritual existence; of which the germ has been implanted in the mind of Man, and which, developed as it is by the mental cultivation that is almost necessary for the formation of the idea, has been regarded by philosophers in all ages as one of the chief natural arguments for the immortality of the soul.

CHAPTER III.

ON THE MINUTE ANATOMY OF THE CONNECTIVE TISSUES. CELLS AND THEIR DERIVATIVES.

42. The whole substance of the body in many of the lower forms of Animal Life, and the elementary parts from which the several tissues are formed in the higher, is composed of a soft gelatinous substance which was named *Sarcode* by Dujardin, *Protoplasm* by Reichert, v. Mohl and Remak, *Cytoplasm* by Kölliker, *Germinal matter* by Beale, and in its various kinds represents the 'Physical Basis of Life,' of Huxley.* It is transparent and homogeneous and may be compared to white of egg. It usually presents a number of minute granules distributed through its substance, which are derived in part at least from the materials it has absorbed. It may exist in the form of separate masses, varying in size from points scarcely perceptible with the microscope, to such as are visible to the naked eye, or in the form of layers or sheets lining the interior of cells and vessels. When at rest it is probable that masses of protoplasm assume a spherical form, but under all ordinary circumstances they are more or less flattened and exhibit certain movements, and present the phenomena of growth, nutrition, and reproduction. The movements witnessed in Protoplasm are of two kinds, both of which are rendered conspicuous by the molecules in its substance. The first is a vibratory, quivering, or dancing movement of the granules resembling closely those trembling movements of resinous and other inorganic particles suspended in fluids, which, having been first described by Robert Brown, are sometimes called Brownian motions. Such vibratory movements are chiefly seen in spherical masses of Protoplasm, and cease when these are undergoing changes of form or place. The second kind of movement demonstrates the contractility of protoplasm, which, as is shown by experiments on the pigment cells of the Chameleon and various Amphibia,† Fishes, and Cephalopoda in

* The best account of Protoplasm is given by Kühne in his essay entitled "Das Protoplasm," Leipzig, 1864; but the reader may refer with advantage to the essay on Cells by Stricker in his "Manual of Histology," Syd. Soc. Translation, vol. i. p. 1, where the chief authorities on this subject are cited; to Huxley's lecture on The Physical Basis of Life, in his "Lay Sermons and Addresses;" and to Haeckel's work on "General Morphology."

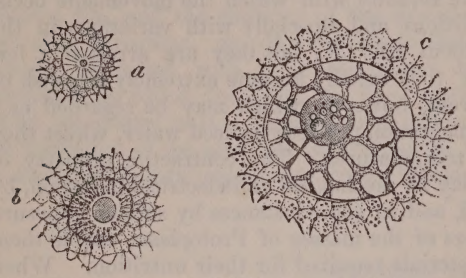
† Lister, "Philosoph. Transact.," 1858.

which the sarcode contains coloured granules, is under the control of the nervous system. The masses change their shape, becoming elliptical or ovoid, and flattened or irregular, owing to the thrusting out of processes, and these may be either withdrawn or may drag the rest of the body after them, so that in detached masses locomotion is effected. The processes may vary in shape from rounded elevations or swellings but slightly projecting from the general surface, to long and extremely delicate threads, and portions may then become altogether detached. The rapidity with which the movements occur differs with the surrounding conditions, and especially with variations in the temperature, being greatest at about 100° F., but they are arrested a few degrees higher (110° F.). At 32° they usually become extremely sluggish or cease altogether. The ova of trout, however, which may be regarded as a kind of Protoplasm, undergo segmentation perfectly in iced water, whilst they soon cease to move at ordinary temperatures. The contractile property of Protoplasm can be brought into play by mechanical and electrical irritation, by the application of chemical stimuli, and in some instances by sudden exposure to light.* The locomotive powers of the masses of Protoplasm enable them to search for, and procure, the materials required for their nutrition. When such materials are met with, the Protoplasm extends itself over and embraces them, the opposite surfaces coalescing, so that the foreign body is entirely included; its nutritive parts are then extracted, and the remainder, if any, is cast away by the retreat of the Protoplasm from it. The reproduction—or rather multiplication—of such masses is effected by the detachment of a larger or smaller portion of the parent mass, the two parts separating to obtain the substances requisite for their own growth and nutrition. Chemical examination of Protoplasm shows that it contains a considerable proportion of myosin, and in some instances, protagon, glycogen, and cholesterin have been found to be present. Protoplasm, presenting slight but unimportant differences from the general description above given, is found to form the contents of all Vegetable cells, at least in their early condition, to constitute the essential part of a great group of organisms which have been associated together by Haeckel under the name of Protista, and include such forms as the Flagellata, Diatomaceæ, Myxomycetæ, and Foraminifera, the last of which recent researches have shown to form a thin, but very widely spread, layer on the bed of the ocean at all depths. And, finally, it forms the living material in the interior of all animal cells, and to its presence the active processes they exhibit are essentially due. In the very simplest forms of Animal Life, as in the Monera, no differentiation of structure is visible in the Protoplasm of which they are composed. But in most of the Amœbæ and Foraminifera; in the ovum at an early stage of its development; in the free floating corpuscles known as the white corpuscles of the blood; in granulation cells and pus corpuscles; in the corpuscles of the ductless glands; in osteoblasts, and elsewhere, the small masses of Protoplasm contain a nucleus; and such bodies may be conveniently designated by the term employed by Haeckel of *Plastids*. In most cases the outer surface of the Protoplasm has undergone a certain, though often very slight, degree of consolidation. And when this consolidation has proceeded so far as to form a thin membrane around the protoplasmic mass and nucleus, an *encased cell* is formed, the mature forms and characters of which differ considerably in plants and animals, though the history of their development is nearly the same.

* Engelmann, Pflüger's "Archiv," 1879, Band xix. p. 1. F. Darwin, "On the Contractile Filaments of the Teasel and of Amanita," in "Quart. Journ. of Mic. Sci.," July, 1877, and January, 1878, p. 74.

43. The observations of Strasburger* have shown that in the evolution of the *vegetable* cell the nucleus first appears as a simple point. Around this as a centre a transparent spheroid of protoplasm forms (Fig. 12, *a*), the outer surface of which becoming slightly condensed, constitutes the limit of the newly formed cell.† As this increases, a new distribution of the protoplasm occurs, which becomes reticulated (Fig. 12, *b*), a thinner fluid, or cell-juice, occupying the meshes. The nucleus, originally spheroidal, changes its form and position, becoming oval or discoid, and more or less eccentric (Fig. 12, *c*). The young cells at first separate, approximate to each other, and at length touch at certain points; and wherever this occurs a lamella of cellulose is deposited between them—a substance which ultimately encloses the whole cell. The cell is now complete. The nucleus appears to represent the cell on a smaller scale, having its own limiting membrane and its own reticulated protoplasm. All evidences of activity in cells are due to the protoplasm they contain; for if this be reduced to inactivity by desiccation, by exposure to moderate heat, or by withdrawal of oxygen, the cell remains quiescent, and no secretory, motor, or other form of activity is exhibited. In compound organisms composed of many cells every cell, in maintaining its own nutrition, ministers to the functional activity of the special tissue to which it belongs, and is subservient to the wellbeing of the organism at large.

FIG. 12.



Free-cell development exhibited in the growth of the cells of the albumen of *Phaseolus multiflorus*.

a, represents an early stage of development. The nucleus is seen to be still punctiform and the cell is represented by a clear spheroid slightly granular in the interior, and limited by a well-defined line.

In *b*, the nucleus has become vesicular, the protoplasm of the cell presents a reticulated aspect.

c, represents a fully-developed cell. The nucleus is vacuolated, the protoplasm is more distinctly differentiated into a reticulated tissue containing the cell-juice in its meshes; the cell-wall presents a double contour.

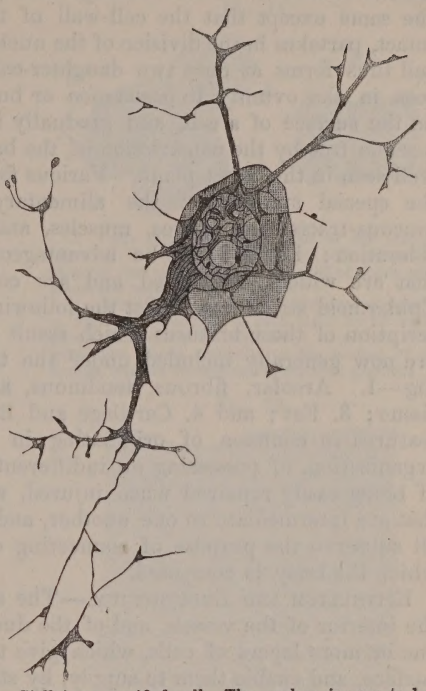
44. The structure of an *animal* cell is essentially similar to that of a vegetable cell, and they frequently arise in the same way. When mature it is composed of a more or less firm and consistent limiting membrane, apparently composed of some modification of protoplasm representing the cellulose *cell-wall* of the Plant Cell, and like it enclosing a reticulated mass of protoplasm—a nucleus and cell-contents which vary with the organ from which the cell has been taken. The consistence of the cell-wall may, as in the case of the hepatic cells, be only slightly, if at all, denser than the general protoplasm of the cell, or, as in cartilage cells, it may acquire great firmness and thickness. Occasionally it presents pores, as in the ovum of the Fish and the cells of the notochord; and it may be deficient at some part of the surface, as in the cells covering the intestinal villi. It is often prolonged in the form of cilia, or of processes rendering it more or less stellate in form. A *nucleus* is rarely, if ever, absent in young cells. It may be spheroidal, oval, fusiform, or discoid in shape, and may be centric or eccentric (Fig. 13). It consists of a delicate sac, the cavity of which is traversed by numerous anastomosing fibres. According to the closeness and form of the fibres, the appearance presented is that of a net, or the honeycombed aspect of a sponge. In either case the meshes of the nuclear plasma are filled with nuclear juice. The

* "Ueber Zellbildung und Zellthielung," Jena, 1875.

† The primordial utricle of Hofmeister.

ibres often present slight thickenings at certain points, as well as bright pots, which are the expression of the optical sectional view of the fibres, whilst at other points the meshes are loser, giving rise to local thickenings which Klein believes to be the nucleoli; a view that is not incompatible with the spontaneous movements hat have been observed in them.* The *contents of cells* like those of he nucleus are generally divisible nto two parts, Protoplasmic substance which appears in the form of granular anastomosing filaments, bands, or nembranes traversing the interior, and extending from the outer surface of the nucleus to the periphery of the cell; and Paraplasm, which varies in characters and attributes with the special tissue or organ from which he cell has been taken, being sometimes transparent and colourless, sometimes charged with pigment, and sometimes containing the special secretion of a gland; in some instances he protoplasm seems to become almost wholly replaced by fat, or acquires he highly differentiated properties of nerve or muscle. In young cells, the protoplasm is mingled with cholesterin and lecithin, and in many instances with glycogen. The mode of origin, or genesis, of cells varies in different instances. The method to which reference has just been made is termed *free-cell formation*, the cells developing independently in a blastema that has been formed by pre-existing cells. It is seen in the Myxomycetes,† and Legros and Onimus‡ and Montgomery§ have shown that it also occurs in the higher animals, since, if small sacs made of goldbeater's skin or parchment-paper be filled with the serum of a blister, filtered to remove all morphological elements and placed beneath the skin of a rabbit, a large number of leucocytes appear in the fluid in the course of twenty-four hours. This mode of development is, however, comparatively rare, and animal cells in general arise by one of three methods, by endogenous multiplication, by fission, or by germination.

Fig. 13.



Stellate or ramified cell. The nucleus is seen to be vacuolated, the protoplasm forming a network which contains a clear juice in its nucleus.

In *endogenous multiplication* the nucleus primarily divides into two, then into four, eight, or more parts, each segment attracting around it a spheroidal portion of the protoplasm of the mother-cell. The mother-cell usually grows

* By Auerbach, "Organolog. Studien," Breslau, 1874. Brandt, "Archiv. f. Mit. Anat.," Band x. Eimer, idem, Band xi. Kidd, "Q. J. Mic. Sci.," 1875, p. 133. Klein observed that the meshes of the intra-nuclear fibres are closer and more compactly arranged near the periphery of the nucleus forming an internal filamentous membrane, sometimes separated by a hyaline space from the proper membrane of the nucleus. The nucleus as a whole has been observed under favourable circumstances to execute movements of an amœboid character. (Kidd, op. cit. p. 133.)

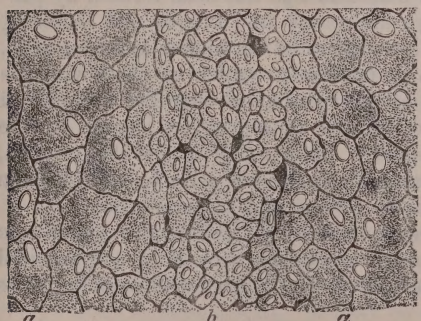
† De Bary, "Die Mycetozoen," 1864.

‡ "Journal de l'Anatomie," 1867. § Idem, 1868.

to some extent; but the daughter-cells growing more rapidly, ultimately burst the resisting membrane that confines them and are set free. This method is seen in fat and cartilage cells (Fig. 31). In *fission*, the process is the same except that the cell-wall of the parent-cell instead of remaining intact, partakes in the division of the nucleus and cell-contents, and the mother-cell thus forms at once two daughter-cells. This method of development is seen in the ovum. In *gemmation* or budding, one or more swellings appear on the surface of a cell, and gradually increasing in size are nipped off and become free by the constriction of the base. This method of development is well seen in the yeast plant. Various forms of cells will be described when the special subjects of the alimentary, respiratory, and genito-urinary mucous-tracts, the nerves, muscles, and glandular organs are under consideration; but it will be advantageous to consider here various forms that are widely distributed and are collectively known as Epithelial and Epidermoid structures, whilst the following sections will be devoted to the description of those textures which result from the metamorphosis of cells, and are now generally included under the title of Connective Tissues, embracing—1. Areolar, fibrous, tendinous, and ligamentous tissues; 2. Elastic tissue; 3. Fat; and 4. Cartilage and Bone. These tissues all present the features in common of originating in cells, of presenting a low type of organization, of possessing an indifferent supply of bloodvessels and nerves, of being easily repaired when injured, whilst they frequently present forms that are intermediate to one another, and finally, as their name implies, they all subserve the purpose of connecting or supporting the other textures of which the body is composed.

Epithelium and Endothelium.—The skin, mucous and serous membranes, the interior of the vessels, and of the ducts of many glands, are covered with one or more layers of cells, which give to these parts a smooth and uniform surface, and enable them to supply, by structures capable of easy renewal, the losses they experience from the friction to which they are constantly subject. The innermost recesses of glandular organs are also lined by cells, the function of which appears to be the separation from the blood, or the formation from the materials supplied by that fluid, of the secretion proper to each. Four principal kinds of cells have been distinguished by microscopists, forming by their juxtaposition, tesselated or pavement, cylindrical or columnar, spheroidal or glandular, and ciliated epithelium, and the contours of the cells may be brought into view by immersing the fresh membrane for a few minutes in a one-half or one-quarter per cent. solution of nitrate of silver, and then washing in distilled water.

c Fig. 14.



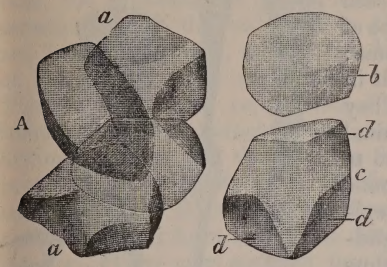
a *b* *a*

Tesselated Epithelium from the abdominal surface of centrum tendineum of rabbit, strongly coloured after treatment with nitrate of silver.—*a*, dark silver lines of the interstitial substance of the endothelial cells; *b*, cell-substance; *c*, nucleus. The smaller cells lie over a capillary lymphatic. The dark spaces are pseudo-stomata.

Tesselated epithelium is found as a single layer of flattened cells in the interior of the vessels and synovial and serous membranes (Fig. 14), and here receives the name of Endothelium. The cells are seen to be flat, and are often either sinuous in outline, or are rendered polygonal by mutual pressure. They possess a cell-wall, and

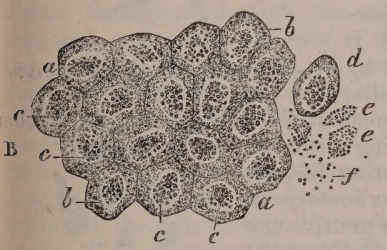
a distinct nucleus, which are best seen after staining with silver nitrate and hæmatoxylin. As a multiple layer this form is well seen in the skin (Fig. 18, *a*, *b*),

FIG. 15.



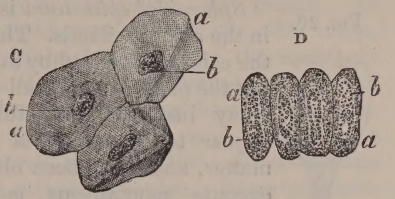
A. Cells of the corneal layer.—*a*, group of lamelliform cells without nuclei, still adherent to each other; *b*, an isolated cell; *c*, another cell presenting the impressions, *d*, *d*, *d*, of the cells with which it was previously in contact.

FIG. 16.



B. Cells of the mucous layer seen from the deep surface.—*a*, *a*, group of cells united by an amorphous substance; *b*, thin envelope or cell-wall; *c*, the nucleus surrounded by pigment granules; *d*, detached cell; *e*, thin nuclei with still adherent pigment granules; *f*, scattered pigment granules.

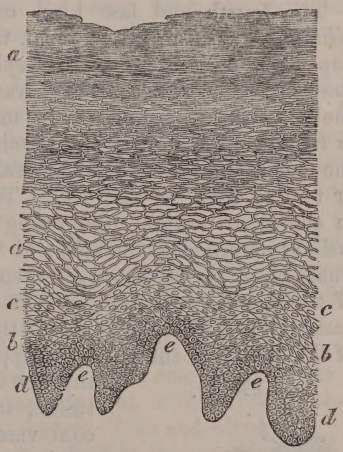
FIG. 17.



C. Cells from the upper part of the mucous layer.—*a*, flattened and lamelliform cells resembling those of the corneal layer; *b*, nuclei of these cells, small and with festooned border.

D. Cells from the deep part of the mucous layer.—*a*, four cells adhering to each other by an amorphous substance; *b*, thin nuclei, which are elongated, are placed vertically to the surface of the dermis, and are surrounded by pigment granules.

FIG. 18.



Vertical section of the epidermis of the skin of the palm of the hand, × 100.—*a*, *a*, thick corneal layer composed of a large number of superimposed cells without nuclei; *b*, *b*, mucous layer formed of nucleated cells; *c*, upper part of this layer which is separated from the corneal layer by an undulating line; *d*, *d*, projections from the inferior surface corresponding to the depressions between the papillæ of the dermis, *e*, *e*.

where it constitutes the thick epidermis. The action of a blister splits the epidermis into two portions; a deeper one—the rete mucosum—in which the cells (Fig. 16, *b*, and Fig. 18, *b*), being in an early stage of their development, are more or less soft and rounded, and remain attached to the dermis; and a superficial portion — stratum corneum or epidermis—which forms the blister, and is composed of flattened cells firmly cohering together (Fig. 18, *a*, shown isolated in Figs. 15 and 17). The cells of the rete mucosum are the chief seat of the pigmentary deposit characteristic of the skin of the Negro and of the darker portions of the body of fair-skinned races. In some parts the cells are serrated at their margin (Fig 19).

FIG. 19.

Epithelial Cell (ribbed cell of the Rete Malpighii).

The second form of cell—the *columnar*—occurs throughout nearly the whole of the alimentary canal. The cells are arranged vertically to the surface, as seen in Fig. 17, D, and are attached to the subjacent membrane by their small extremity. They possess a distinct nucleus,

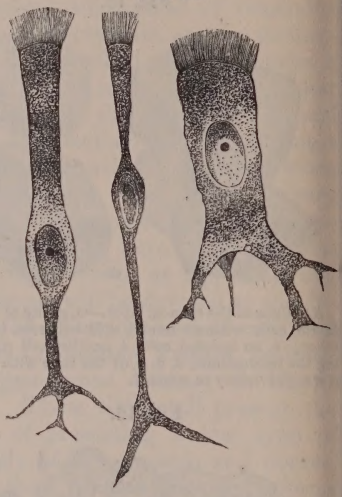
cell-wall, and cell-contents, and their mouth in those lining the small intestines is closed by a striated membrane, the striæ being by some believed to represent fine pores, permitting the passage of oily and albuminous fluids.

Fig. 20.

Cup, or *Goblet-Cell.*

Spheroidal epithelium is best seen in the acini of glands. The shape of the cells is expressed by their name: but the presence of a cell-wall is in many instances doubtful. They appear to be masses of germinal matter, and have been observed to execute spontaneous movements. Both spheroidal and columnar epithelial cells are also capable of gliding over one another, and thus changing their position without becoming detached. The bladder, for instance, when contracted presents eight or nine series of cells, but when distended only two or three.*

Fig. 21.



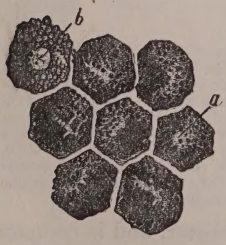
Various forms of *Ciliated Epithelial Cells* from the trachea of a cat.

The fourth and last kind of cell—the *ciliated*—varies much in form, though perhaps the cylindrical or sub-cylindrical is the most common. It is characterized by the presence of a number of minute cilia, or hair-like processes of the contained protoplasm of the cell, which project from the basal border of the cell-wall, varying from one or two to fifty for each cell. These, during life, are in continual motion, performing rapid vibratory or lashing movements, the effect of which is to drive any small body in contact with them towards the outlet of the body. Such cells are found in the respiratory passages, with the exception of the finest ramifications of the bronchial tubes; in the upper part of the vagina, the uterus, and the Fallopian tubes; in the vasa efferentia, coni vasculosi, and first part of the excretory duct of the testis; and lastly, on the choroid plexus of the lateral ventricles and in the central canal of the spinal cord in young animals. In some Vertebrata they also exist near the commencement of the urinary tubuli, and in the frog in the mouth. The cause of the movement is unknown; it

Fig. 23.

Pigment-cells from tail of *Tadpole.*—*a*, *a*, simple forms of recent origin; *b*, *b*, more complex forms subsequently assumed.

Fig. 22.



Cells from *Pigmentum Nigrum.*—*a*, pigmentary granules concealing the nucleus; *b*, the nucleus distinct.

* E. Neumann ("Archiv f. Mic. Anat."), Band xii. p. 570, finds that the œsophagus and upper part of the digestive canal in fœtuses, aged from 18–32 weeks, is covered with ciliated epithelium. A few ciliated cells were also found in the stomach and in a narrow line extending from the epiglottis to the foramen cæcum on the dorsum of the tongue. The cilia are either seated on a homogeneous bright basal border, or on a bright basal border presenting the striation characteristic of the border of the intestinal epithelium, and he thinks the cilia and the basal rods are continuous. Bochdalek observed certain tubes near the foramen cæcum to be also lined by ciliated epithelium.

is remarkable that it should persist long after the general death of the body. A very peculiar form of cell, termed *Cup, or Goblet-Cell* (Fig. 20), appears scattered over parts that are usually covered by columnar and ciliated cells. According to Klein,* they are only the empty shells of the ordinary ciliated cells, the substance of which has undergone conversion into mucin. In certain parts of the body—as in the choroid coat of the eye, the lungs, and bronchial glands, and in the deep or Malpighian layer of the epidermis of the Negro—cells are found, termed chromoblasts, containing *pigment.* The shape of these cells varies from the most regular hexagonal to extremely irregular branched and caudate forms. They usually possess a distinct nucleus, and the melanin is scattered through the otherwise clear protoplasmic cell-contents in the form of minute granules. Some pigment-cells, as those in the skin of the Frog,† are capable of undergoing remarkable changes in their form and in the distribution of the pigment granules in their interior. They may contract into spheroids, or may expand into a stellate form, with numerous irregular, branched, anastomosing, and gradually attenuating processes; and the pigment granules may either accumulate around the central nucleus, or be distributed through the protoplasm. According to Lister, their concentration follows exposure to the action of light, section of the nerve, and the death of the animal. On the other hand, the molecules diffuse themselves through the cell-processes, when the animal is kept in darkness, and when the skin is irritated. Hering‡ and Hoyer think the movements of the granules are essentially dependent upon disturbances or variations of the circulation due to the action of the vaso-motor nerves, by which they are therefore indirectly influenced. Pouchet,§ however, believes he has traced nerve fibrils directly into the sarcodal substance of the chromoblasts.‖ Saviotti¶ has observed the migration of the pigment-cells of the wall of the frog's foot into the bloodvessels after irritation, the time occupied in the transit of the cells through the walls of the bloodvessels being about twelve hours. M. Tschaussow** observed, on the contrary, the passage of a pigment-cell *out* of a vein and its division into two in the tissues. When the cell is crushed the black particles escape and exhibit Brownian vibratory or quivering movements. When viewed singly and with high powers the particles appear transparent and nearly colourless. The colouring matter or melanin is insoluble in water and most reagents, but it dissolves in weak alkalies. It is not bleached by chlorine. It contains iron and nitrogen.

45. *Areolar, Fibrous, and Elastic Tissues.*††—Ordinary *connective tissue* in its fully-developed form may be shortly defined to consist of plasmatic corpuscles scattered through a fibrillar matrix. Amongst the principal examples

* "Handbook for the Physiological Laboratory," 1873, p. 23.

† See the paper of Lister, in "Phil. Trans." 1858; of MM. Hering and Hoyer, in the "Centralblatt," 1869, p. 49; of Brücke, in his "Vorlesungen über die Physiologie," 1874, p. 440; and of G. Pouchet, "Journal de l'Anatomie," 1876, p. 1, who has named such cells 'Chromoblasts.' In some instances the pigment instead of being like melanin in the form of granules, is dissolved in the sarcode, which then presents various shades of red, orange, or yellow. Sulphuric acid has no action on melanin, but changes the tint of the other pigments successively to green, blue, and violet.

‡ "Cbl. f. d. Med. Wiss." 1869.

§ "Month. Mic. Journ." Dec. 1871; and Robin's "Journ. de l'Anat.," 1876, p. 29.

‖ In some instances the coloration perceptible in animal tissues is due to absorption of certain rays, a property that Pouchet has termed *Cœrulescence.* It is to this that the blue colour of the iris is due, the tint of a thin lamina of cartilage, and the reason that the veins appear blue through the skin, though conducting red blood.

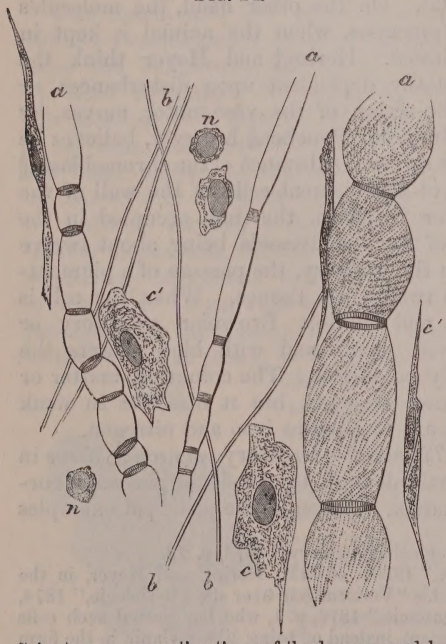
¶ "Centralblatt," 1870, pp. 145 and 161.

** "Centralblatt," 1870, p. 309.

†† For a good account of Connective Tissue see Ranvier, "Traité Technique d'Histologie," 1875-78, p. 325.

of ordinary connective tissue met with in the body we may include the various structures termed tendons, ligaments, fasciæ, aponeuroses, periosteum, and perichondrium; the investing membranes of many organs, as the dura mater, pericardium, tunica albuginea of the testis and of the ovary, and the sclerotic and corneal coats of the eye. It also forms the basis of the dermis, of mucous, serous, and synovial membranes of the chorion, the sheaths and tunics of vessels, of amorphous membranes like the hyaloid humour of the eye, and of the envelopes of glandular follicles. These all present a general similarity of structure and chemical composition, though differing in minor details. Connective tissue may present itself in several forms as, first, *loose connective tissue*, such as occurs beneath the skin. Here, if a small quantity of silver nitrate or staining fluid be injected with a sharp-pointed syringe, and the little œdematous swelling removed and quickly placed under the microscope, it will be seen (Fig. 24) to consist of longitudinally striated fasciculi of connective tissue running in all directions, but separated by the liquid that has been forced in; sharply-defined fibres of elastic tissue, partly running parallel to the fasciculi, and partly coiling round them; large flat cells, fat cells, and small masses of protoplasm resembling the white corpuscles of the blood. The *fasciculi* (*a*) vary from the 1-10,000th or less to 1-2000th in diameter, especially if acetic acid has been added, which causes them to swell up, and exhibit annular or spiral constrictions, corresponding to the lines pursued by the elastic fibres which are not acted on by this reagent. When acted on by picric acid the fasciculi can easily be broken up into their constituent fibrils, which are found to be excessively delicate cylinders. The fasciculi exert a double refractive power on light.

Fig. 24.



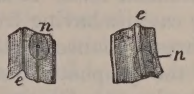
Subcutaneous connective tissue of the dog, prepared by the interstitial injection of a 1-1000 solution of silver nitrate, stained with picrocarminate and mounted in glycerin slightly acidified with a little formic acid.—*a*, connecting tissue fasciculi with annular fibres surrounding them at intervals; *b*, elastic fibres; *c*, flat cells seen *en face*; *c'*, flat cells seen in profile; *n*, lymphatic cells.

The *elastic fibres* (*b*) stain yellow with picric acid and with iodine; they vary greatly in size, branch and anastomose, run straight or in a more or less undulating or spiral manner. They appear to be perfectly homogeneous, and have well-defined dark borders. The quantity present varies considerably in different situations in accordance with the different functions it has to fulfil. The *cells* belonging properly to the connective tissue are nucleated, large, granular and greatly flattened; some are polygonal and regular; others present amœboid movements (*c*); seen in profile they are fusiform. They appear to be attached to and to embrace the fasciculi at intervals. The *fat cells* and *lymphatic cells* are extraneous or accidental elements, and will be described in a subsequent section.

A second form of connective tissue is presented by the *tendons*. These are dense, strong, round or flattened aggregations of connective tissue by

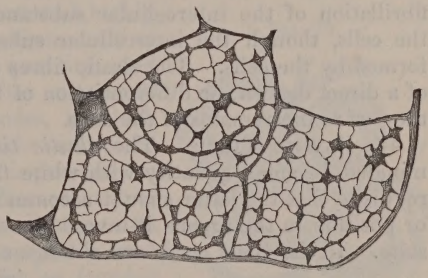
means of which muscles are inserted into bone. They have an external investment of flattened epithelial cells, and are only feebly supplied with blood. On microscopical examination they are found to be composed of fasciculi of connective tissue, the fibres of which run in a nearly straight direction, and are invested by peculiar nucleated cells, which when slightly compressed assume a rectangular form (Figs. 25 and 27.) The cells are curved like the tiles of a house.* The cells present one or more longitudinal ridges (the elastic striæ of Boll, or 'crêtes d'empreinte' of Ranvier) (*e*), which are probably the projections of the cells into the spaces between adjoining fasciculi seen foreshortened, though they may possibly be the result of wrinklings of the cell-wall or of coagulation of the protoplasm. A few fine elastic fibres accompany the tendinous fibres. Transverse sections of tendons exhibit such stellate figures as are shown in Fig 25, and which were considered by Virchow to be formed by branched and anastomosing plasmatic cells, and to constitute channels for the conduction of nutritive fluid; though Henle regarded them as merely representing the interspaces between the parallel fasciculi of the tendon. Ranvier, the most recent inquirer, considers them to be the sections of the cells that have just been described. In the case of the serous and synovial membranes, which as Klein has shown may be regarded as dilatations of the lymphatic system, the connective tissue is so arranged as to constitute bags or sacs, the inner surface of which is, for the most part, lined by a single layer of flattened epithelial cells, forming an exquisitely smooth and polished surface, that materially facilitates the constant gliding movements to which these parts are subjected. Besides these, more rounded cells, termed 'germinating endothelial cells' by Klein, are found in certain regions, as will be more fully explained in the section on the lymphatic system. In the vitreous humour of the eye, and in the substance which constitutes the greater part of the umbilical cord, there exists a peculiar form of connective tissue, termed *mucous* or *gelatinous tissue*. The structure of the vitreous humour of the eye is difficult to determine, but it appears to be composed of a jelly-like fluid, contained in the meshes of a network of exquisitely fine filaments; it is doubtful whether any cells are present. In the cord the matrix is soft, transparent, and homogeneous as in the vitreous, but

Fig. 25.



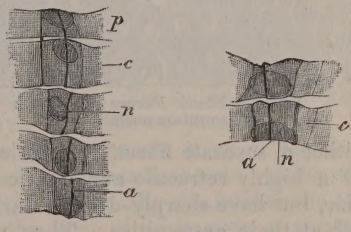
Two isolated cells from the tendon of the tail of a rat. Treated with osmic acid and picrocarmin, then teased out with needles, and mounted on glycerin.—*n*, nuclei; *e*, longitudinal ridges (crêtes d'empreinte of Ranvier, × 356).

Fig. 26.



Tranverse section of *Tendon*, showing branched cells, enclosing spaces which, here left blank, are naturally filled with tendinous fasciculi.

Fig. 27.



Cells of the tendons of the tail of a mouse. —*c*, cells; *p*, lateral processes; *n*, nuclei; *a*, longitudinal ridges (crêtes d'empreinte of Ranvier).

* And have hence been compared to the paddle-wheel of a steamer, the connective tissue occupying the re-entering angles between the laminæ, and the nucleus being contained in the chief lamina. See Waldeyer "Archiv. f. Mic. Anat.," Band xi. p. 176; also Dr. Karl Mays, "Virchow's Archiv.," 1879, Band lxxv. p. 128, in which the bibliography of this subject is well given.

presents round, fusiform, or stellate cells, with branched and communicating prolongations scattered through it. This kind of connective tissue is found only in embryonic structures, or in organs retaining their embryonal characters. In mucous membranes the layer of connective tissue is much thicker and more vascular than in serous, frequently contains minute glands, and instead of a single layer, is covered by many layers of epithelial cells, of a more or less rounded or columnar form. In all instances mucous membranes constitute the walls of tubes or cavities having free outward communication. The interspaces between the fibres of connective tissue are believed by many to constitute the commencement of the lymphatic system, receiving the superfluous material poured out by the bloodvessels for the supply of the several textures, and gradually conveying it, at first through irregular spaces partially filled with protoplasmic masses or cells, but subsequently through proper tubes, to the thoracic duct, from whence it is again discharged into the blood. On boiling with water this tissue yields gelatin. The connective tissue is primarily developed from the mesoblast. Much difference of opinion exists in regard to the mode of origin of the fibres; some thinking that they are derived from the elongation and fibrillation of the protoplasm of the cells, whilst the recent observations of Ranvier seem rather to show that they result from the fibrillation of the intercellular substance without the direct participation of the cells, though the intercellular substance itself was of course originally formed by the cells. The elastic fibres are commonly believed to be the result of a direct deposit, or differentiation of the matrix, though Virchow thought they were the remains of the cells.

46. Elastic Tissue.—The *elastic tissue* that we have just seen to be mingled in small quantity with white fibrous tissue in situations where it is requisite that the latter should accommodate itself to changes of form, bulk, or position in the organs it invests, is sometimes met with in an almost pure state. In the vocal cords and the ligamenta subflava good examples are seen of this tissue, with scarcely any intermixture of white fibrous tissue. In the ligamentum nuchæ and the suspensory ligament of the penis, in the stylo-hyoid, thyro-hyoid, and crico-thyroid ligaments, and in the coats of the bloodvessels and lymphatics, both kinds of tissue are present in nearly equal proportion, though perhaps the elastic predominates; whilst in the subcutaneous and submucous areolar tissue, the elastic fibres, though numerous, form only a small part of the general mass. When examined under the microscope it is found to consist either of separate fibres, of bundles of fibres, or of broad membranous bands of a highly refractile and elastic substance. The fibres vary indefinitely in size, but have sharply-defined dark borders, and appear to be abruptly broken off at their extremities. They may anastomose and branch, and where the fibres are broad and membraniform, and the anastomoses close, a thin tissue results, as in the lining or fenestrated membrane of the arteries, which presents a continuous sheet with only here and there minute holes or spaces. The arrangement of its bloodvessels and nerves, which are very few in number, is not accurately known. The fibres are reddened with Millon's reagent, and give the xanthoproteic reaction. They are not acted on by

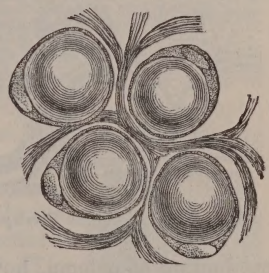
Fig. 28.

Yellow or *Elastic Fibrous Tissue*, from ligamentum nuchæ.

acetic acid. When long boiled they yield a little modified gelatin. Elastic tissue fulfils important functions in the vascular system—to which attention will hereafter be called—and it frequently occurs in situations where its physical properties enable muscular tissue to be dispensed with, as in the ligamentum nuchæ of the larger quadrupeds. Occasionally, though more rarely, it appears as the antagonist of muscular effort, as in the chordæ vocales, and typically in the hinge of the shell in the Lamellibran chiata.

47. Adipose Tissue.—This form of tissue is extensively distributed through the animal kingdom, and consists of large cells filled with oil, which in good specimens are individually separated from one another, as well as collected into lobules by delicate trabeculæ of connective tissue (Fig. 29). It is more freely supplied with blood than most of the other forms of cellular or connective tissue, and according to Toldt the one or two arterial branches distributed to a given lobule do not communicate with those of adjoining lobules, whilst the blood is returned by a pair of veins accompanying the arterioles. The cells, though varying much in size, average the $\frac{1}{500}$th of an inch in diameter, and are rendered polygonal by mutual pressure; they are composed of a cell-wall of considerable thickness, lined by a layer of protoplasm, in which an eccentric nucleus with several nucleoli is imbedded, and which surrounds a clear, perfectly transparent, and highly refractile drop of oil. The connective tissue uniting the lobules is sometimes small in quantity, and exceedingly delicate, as in the fat that surrounds the kidney, and in the marrow of bones, in which free-cells may be observed; whilst in other instances, as in the subcutaneous layer of fat, it is possessed of much firmness, and is very dense. Nerves may be observed to accompany the vessels distributed to fat lobules, but their mode of termination is unknown.* Toldt describes the lymphatics of fat as forming wide-meshed capillary plexuses, but has been unable to discover that they possess any definite arrangement. Adipose tissue is absent in the brain, lungs, liver, and in the delicate skin of the eyelids, of the prepuce, scrotum, and nymphæ. In all these regions, however, oily globules may be seen on making fine sections. The absolute amount of fat in a well-nourished man amounts to about $\frac{1}{20}$th of the weight of the body. Infancy, mid-age, warmth, abundant food, especially of a saccharine or oleaginous nature, freedom from mental anxiety, castration, indolent habits, and inherited constitutional peculiarities, are all circumstances predisposing to the accumulation of fat. It is probable that every form of cell may become infiltrated with fat, as a stage or form of degeneration. Fat fulfils the following important objects in the animal economy:—It diffuses pressure, and is, therefore, largely developed on the palms of the hands, soles of the feet, buttocks, and female breast. By its disposition beneath the skin generally, it forms a warm investment for the body that materially diminishes the loss of heat by radiation and conduction; at the same time it gives a smooth, flowing, and agreeable contour to the surface which otherwise, especially near the joints, would present hard and angular outlines. It forms an elastic pad, or cushion, in the orbit, on which the eye can rotate; and in the heart, by filling up the interstices of the vessels and the irregularities of its surface, it fulfils a similar function, enabling this organ to perform its ceaseless move-

Fig. 29.



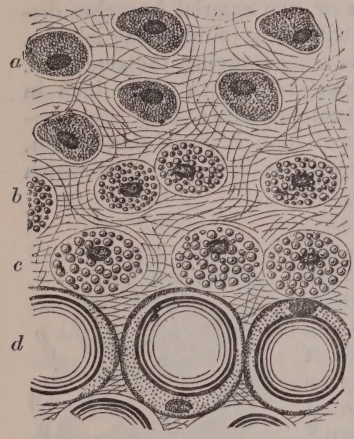
Four fat cells, with intervening connective tissue.

* Toldt, "Lehrbuch der Gewebelehre," 1877, p. 180.

ments with the least possible amount of friction. It confers lightness, and probably a certain degree of elasticity, on the bones—as well, indeed, as on all other tissues into the composition of which it enters. It constitutes a storehouse or reserve fund of hydrocarbonaceous material, which, when required by the economy, can readily be absorbed into the blood; the process of absorption being facilitated—as Matteucci has shown—by the alkalinity of the fluid that moistens the outer surface of the cells. Lastly, if we may judge from its constant presence when these processes are taking place, it plays an important part in the acts of nutrition, growth and development. Its sp. gr. is 0.924.

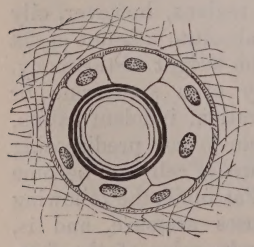
According to M. F. Czajewicz,* the cells of adipose tissue originate in the corpuscles of ordinary connective tissue. These, in any part that is about to become the seat of the deposit of fat, increase in size, assume a spherical form, and become filled with a mist of small fat drops (Fig. 30, *a*). At a stage slightly more advanced (*b*), the mist becomes condensed into small drops, which gradually acquire a larger size and greater distinctness (*c*), and ultimately blend into one large oil globule (*d*). Toldt, however, maintains that fat cells in the earliest stages of their development have no cell-wall, and constitute a tissue quite *sui generis* and distinct from connective tissue. In the later stages, the nucleus of each corpuscle, though still discoverable on careful examination, is generally pressed to one side, and is to a great extent obscured by the oily contents of the cell. Experiments made with picrocarminate of ammonia, or by means of the artificial production of œdema, however, not only demonstrate its presence, but also that it is surrounded by the remains of the protoplasm originally filling the cell, which expanded by the oil globule forms a thin layer beneath the secondary cell-wall, and which may be regarded as still playing an active part in the deposition or absorption of the oily matter.† When an animal is starved the oily material is continuously withdrawn from the cells, and its place is supplied by a serous fluid, the cells still preserving their round form. If now abundant food be given, a series of changes similar to those above described may be observed, the cells becoming filled at first with minute oil globules, which afterwards coalesce to form one of large size. If inflammation is established in adipose tissue by the injection of solution of iodine, or other irritant, the endogenous formation of cells can be very distinctly seen (Fig. 31). After death the cells often present crystalline stellæ.

Fig. 30.



Successive stages in the *Development of Fat.*

Fig. 31.



Example of *Endogenous Cell-formation.*

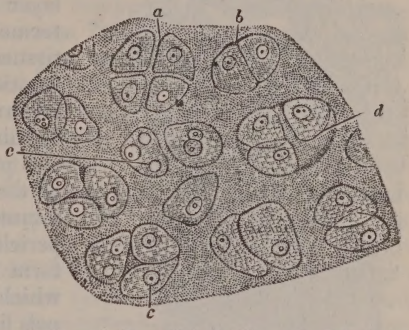
48. Cartilage.—Cartilage presents two forms: the temporary and the permanent; the former exists in considerable quantity in the fœtus, making its first appearance in the vertebral column between the sixth and eighth week of fœtal life, and subsequently occupying the position and constituting the founda-

* Reichert's "Archiv," 1866, Heft iii. p. 289.

† Ranvier, 'Histologie du Système Nerveux," t. i. p. 117.

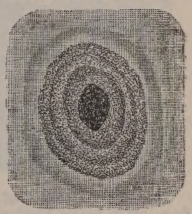
tion of the principal bones of the skeleton, certain portions of the vault of the cranium alone being excepted. The permanent or hyaline cartilage of adults is well exemplified in the cartilage covering the articular surfaces of bones, in the costal cartilages, and in the cartilaginous rings of the trachea. In all these situations it consists of a translucent bluish or yellowish solid mass, possessing great elasticity, and composed essentially of cells distributed through a matrix (Fig 32). The *Cells* are masses of protoplasm, and are contained in cavities named chondroplasts, which they completely fill. In the earlier periods of development, when the tissue is named *embryonal* cartilage, the cells are spheroidal and nucleated, and are almost in contact with each other; but in the later periods of development, in what is termed *fœtal* cartilage, the matrix or intercellular substance is much increased in quantity, and the cells become more or less compressed from mutual pressure. In *adult* cartilage an investing capsule (Fig. 33) forms around the cell which separates it from the matrix, and often presents concentric layers. Under certain circumstances the cells of cartilage have been observed to perform movements—contracting, for example, when an electric current is transmitted through them, or when sections are exposed to the action of water; but such movements are at most but slight and feeble. Near the margin of articular surfaces, and in close proximity with synovial membrane, the cartilage cells not unfrequently present transitional changes of form into the cells of connective tissue.* The cartilage capsules near the surface in articular cartilage are capable of being injected with coloured fluids, and therefore possess juice-canals communicating with the surface; and when the pressure is increased it is believed by some† that fine canals may be brought into view effecting a communication between neighbouring capsules. The *matrix* in the permanent or *hyaline* cartilages of the joints appears at first sight to be a homogeneous and structureless material; but by special treatment, as with a 10 per cent. solution of common salt, baryta water, and some other reagents, a fibrillar structure is brought into view.‡ Ordinary articular cartilage is thickest where the pressure is greatest, and the cells are found to be somewhat flattened near the free surface, irregularly distributed in sets of from four to eight or more near the centre, and perpendicularly placed in that part which lies nearest the bone. Embryonal cartilage is always isotropous, as is also the middle layer of articular cartilage; but the superficial and deep layers are doubly refracting.§ In the elastic or reticulated cartilage of the ear, epiglottis, and cartilages of Santorini and Wrisberg, the matrix is of a yellowish colour, and pervaded with elastic fibres (Fig. 34). From this form of tissue the transition is easy to the *fibro-cartilages* exemplified

FIG. 32.



Section of *Branchial Cartilage of Tadpole.*—*a*, group of four cells, separating from each other; *b*, pair of cells in apposition; *c*, *c*, nuclei of cartilage-cells; *d*, cavity containing three cells.

FIG. 33.



Elementary part from *Cartilage of Frog*, treated with carmine, showing successive stages of conversion of germinal matter into matrix.

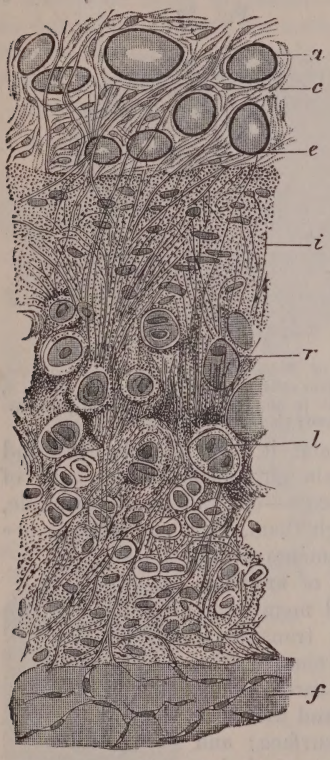
* Ogston, "Journ. of Anat. and Phys.," vol. x., 1875, p. 49.

† Heitzmann, "Jahrb," 1872, p. 339; Budge, "Archiv. f. Mic. Anat.," Band xiv., p. 54; Bubnoff, "Sitz-ber. d. K. Akad. zu Wien," 1868; Ranvier, "Traité Technique," 1877, p. 288.

‡ Baber, "Journ. of Anat. and Phys.," vol. x., 1875, p. 113. § Ranvier, loc. cit. p. 270.

in the symphysis pubis, the intervertebral substance, the interarticular cartilages of the knee and other joints, the glenoid and cotyloid ligaments, and the cartilages lining the grooves for tendons; in all of which the matrix is almost entirely converted into firm and close-set interlacing connective tissue fibres. The costal, as well as the fibro-cartilages are invested by a dense layer of connective tissue, containing vessels termed the periosteum; and although the two tissues may be separated by prolonged maceration, they are structurally continuous with one another. The nutrition of cartilage when in thin laminæ is sufficiently provided for by the process of imbibition; but in the case of the thicker masses it is effected partly by minute vessels which, proceeding from the perichondrium, dip into its outer surface and form loops, and partly by larger branches which traverse its substance, and lie in channels lined by a process of the perichondrium. The tissue is, however, essentially extravascular. No nerves or lymphatics have been hitherto traced into the substance of cartilage; and it appears to be nearly insensible. The exquisite pain accompanying ulceration of joints is probably referable to irritation of the nerves supplying the subjacent bone. On drying it loses about 70 per cent. of water; on being subjected to prolonged coction in water it yields chondrin. The organic basis from which the chondrin is derived constitutes about 30 per cent. of fresh cartilage; and the inorganic substances, of which the sulphates of potash and soda constitute the major part, do not amount to more than 2·5 per cent. (Hoppe-Seyler). The inorganic constituents of rib and knee-joint cartilage differ remarkably.* Permanent cartilage is employed in the construction of the body chiefly on account of its resiliency, as in the ribs, trachea, and bronchi, and the joints. In the latter situation its smoothness, rendered greater by the synovia, prevents free movement and reduces friction.

Fig. 34.



Transverse section of the epiglottis of a dog, after being hardened in alcohol, and subsequent treatment with picrocarmin, mounted in glycerin.—*a*, fat cells; *c*, loose connective tissue; *e*, elastic fibres; *i*, superficial layers of cartilage with small cells; *r*, central portion with large capsules (one of which is indicated by *l*), and a matrix containing fibres and elastic grains; *f*, fasciculi of connective tissue seen in section, magnified 170 diam.

49. Bone.—The bones constitute the organs of support for the softer tissues; and, with the muscles, form a system of levers by which locomotion, prehension, mastication, and various other movements are effected. They more or

* One hundred parts of the ashes contain:

	In Rib Cartilage.	In Knee-joint Cartilage.
Potassium sulphate	26·66	·0
Sodium sulphate	44·81	55·17
Sodium chloride	6·11	22·48
Sodium phosphate	8·42	7·39
Calcium phosphate	7·88	15·51
Magnesium phosphate	4·55	

(Hofmann, "Lehrbuch du Zoochemie," 1879, p. 25).

less perfectly enclose the cavities of the head, chest, and pelvis; and by their hardness and elasticity constitute an efficient protection to the important organs therein contained. They are divided, according to their form, into long, short, irregular and flat bones. In the long bones the shaft is pierced by a central canal, which runs continuously from one extremity to the other; and the hollow cylinder which surrounds this is very compact in its structure. On the other hand, the dilated ends of the bone are composed of a spongy or cancellated structure, which is made up of osseous lamellæ and fibres interwoven together. The arrangement of these is by no means irregular or fortuitous, but exquisitely adapted for the mechanical functions the bones have to perform, and in exact accordance with theoretical requirements;* a multitude of minute chambers or cancelli freely communicating with one another and with the cavity of the shaft being formed, whilst the whole is capped with a thin layer of solid bone. In the flat bones of the head, and less distinctly in the scapula and ilium, we find the two surfaces composed of solid osseous texture, with more or less of cancellated tissue called the *diplöe*, interposed between the layers. This, however, is sometimes deficient, leaving a cavity, as in the frontal sinuses. Finally, we frequently meet (especially in the ethmoid and sphenoid bones) with thin lamellæ of osseous substance resembling those which elsewhere form the boundaries of the cancelli. These consist of a single layer of osseous substance, and are not penetrated by vessels, but are nourished by those ramifying on their surfaces; and they consequently exhibit the elements of the osseous substance in their simplest form. It will be desirable, therefore, to commence with the description of these.

50. When a thin natural lamella of this kind is examined, it is found to belong to the doubly refracting tissues, and to be chiefly composed of a nearly homogeneous indistinctly fibrous substance. Scattered through this are a number of dark spots presenting an oval form, and giving off from their sides and extremities numerous radiating processes of extreme minuteness, and frequently of considerable length. The dark spots are small cavities termed *lacunæ*, and the branched processes, or *canaliculi*, are tubular channels, which, though far too small to convey blood corpuscles, yet, through the agency of the protoplasm, bring the fluid elements of the blood, or matters secreted from them, into close relation with every part of the tissue. The size of the lacunæ is to some extent proportionate to that of the blood corpuscles, being large in reptiles and fish, and smaller in the higher classes of vertebrata. In man their long diameter is about 1-1800th of an inch, and their short 1-6000th of an inch. Every lacuna is occupied in the living bone by a mass of protoplasm which sends prolongations into the canaliculi, and is the nutritive centre of the surrounding osseous substance. If, instead of a thin lamella of bone, sections of one of the long bones be examined, it will be found that the penetration of the tissue by bloodvessels renders a peculiar arrangement of the lacunæ and canaliculi requisite. The solid osseous texture which forms the shaft is covered by a strong and firm layer of connective tissue termed the 'periosteum,' in which numerous bloodvessels ramify, and is lined by a very thin and delicate layer of the same tissue,

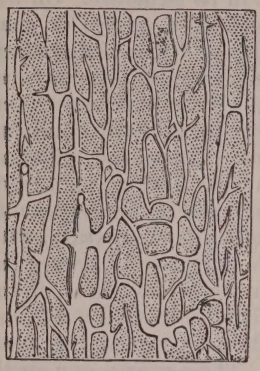
FIG. 35.

Lacunæ of *Osseous Substance*, magnified 500 diameters.—*a*, central cavity; *b*, its ramifications.

* See Meyer, "Die Architectur der Spongiosa," Reichert and Dubois-Reymond's "Archiv.," 1867; Wolff and Culmann, "Die Graphische Statik." Zurich, 1866.

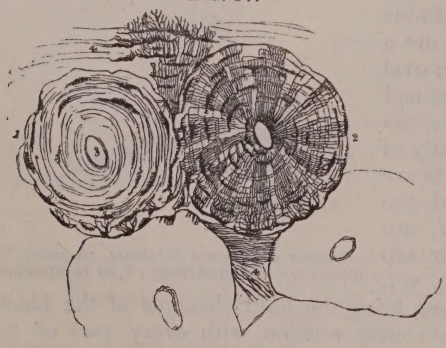
to which the term 'endosteum' is applied. This also is freely supplied with small vessels derived from the nutrient artery or arteries of the bone. From both the external and internal membranes numerous small bloodvessels penetrate the bone, occupying a series of canals that were first described by Clopton Havers, and have been named after him the Haversian canals. These, for the most part, run parallel to the central cavity, communicating, however, with one another by frequent transverse branches, so that the whole system forms an irregular network, and pervades every part of the solid texture (Fig. 36). The diameter of the Haversian canals varies from 1-2500th to 1-200th of an inch or more; their average diameter may be stated at about 1-500th of an inch. The Arteries and Veins usually occupy separate channels, and those enclosing the latter are, in some instances, as in the diploë of the flat bones of the skull, of extraordinary amplitude. In transverse sections the longitudinally running canals appear as circular spaces surrounded by from five to ten or more concentric lines named 'Haversian lamellæ.' Between the lamellæ the lacunæ are seen as dark, white, or open spaces, according to the mode of preparation and illumination (Fig. 37). Besides the lamellæ just mentioned others are seen which run parallel to the medullary cavity, and to the external surface of the bone, and have hence been named 'perimedullary' and 'peripheric' systems of lamellæ. Lastly, a few lamellæ are seen which are not conformable to either of these systems, but occupy their interspaces. Such 'intermediary' lamellæ are the remains of old Haversian systems which have been gradually removed by absorption. The lamellæ form the proper substance of the bone, being composed of ossein impregnated with calcareous salts. If the salts be removed by maceration in acid the lamellæ present a well-marked fibrous structure, the fibres being transparent and decussating with each other to form an extremely delicate trellis-work. The outermost or peripheric lamellæ are often bolted together by perforating fasciculi of fibres, partly white connective tissue, and partly elastic tissue, apparently continuous with the deep surface of the periosteum. Each lamella presents a thinner transparent and homogeneous zone, and a broader, darker, and more granular zone. The lacunæ are situated in the transparent zone.* The dark zone

Fig. 36.



Vertical section of *Tibia*, showing the network of Haversian canals.

Fig. 37.

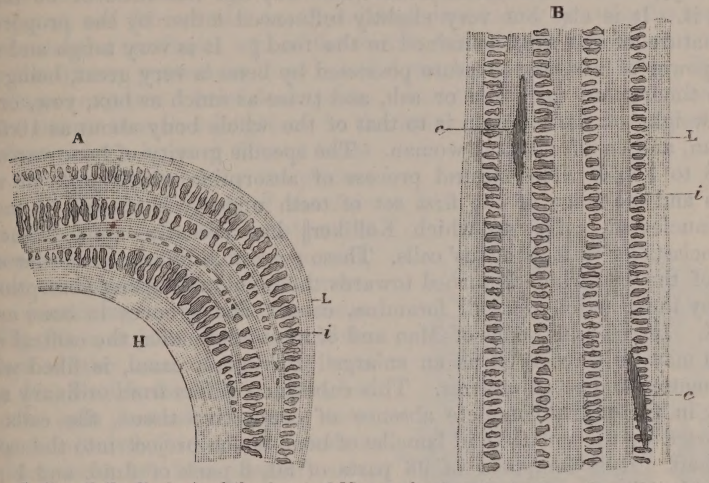


Minute structure of *Bone*, as shown in a section cut transversely to the direction of the Haversian canals:—1, one of the Haversian canals surrounded by its concentric lamellæ: the lacunæ are seen between the lamellæ, but the radiating tubuli are omitted; 2, an Haversian canal with its concentric laminæ, lacunæ, and radiating tubuli; 3, the area of one of the canals; 4, 4, intervening lamellæ; between these lamellæ at the upper part of the figure, several very long lacunæ with their tubuli are seen. In the lower part of the figure the outlines of two other canals are given, in order to show their form and mode of arrangement in the entire bone.

* Sharpey, "Introduction to Quain's Anatomy," 7th Edit. p. xcvi.; Schäfer in idem, 8th Edit. p. 86; and "Quart. Journ. of Mic. Sci.," April, 1878, p. 132.

shows a multitude of short bright lines running radially across it, with dark angular particles between them (Fig. 38). It is not easy to define the limits of a lamella. Sharpey includes both a light and a dark zone in a single lamella, and considers the dark spots to be produced by the cut-ends of the reticulating fibres of which the lamellæ are composed. Schäfer, after com-

Fig. 38.



Section of the diaphysis of the femur of Man, made when the bone was dry and kept in balsam just sufficiently melted to enter into and obliterate the lacunæ.—A, transverse section; B, longitudinal section; H, Haversian canal; L, homogeneous lamellæ; *i*, striated lamellæ; *c*, bone corpuscle. 600 diam.

paring osseous with corneal tissue, defines a lamella as a layer of reticulating fibres covered on both surfaces by a homogeneous substance which extends between the fibres, the plane of separation between two lamellæ being indicated in the fully-formed bone by the presence of flattened lacunæ. The decussating fibres of Sharpey he considers to be the persistent osteogenic fibres. A somewhat different explanation of the same appearances is given by Ranvier, who describes the lamellæ as being alternately clear, or homogeneous and dark, or striated (Fig. 38). He considers the striated lamellæ to be composed of minute connecting rods or bridges with sinuous borders, which extend from one homogeneous lamella to another. This structure, he points out, is apparent both in longitudinal and in transverse sections. If a bone be burnt the organic material that enters into its composition is destroyed, whilst if it be exposed to the action of dilute acid the whole of the salts may be removed, leaving it in a soft and flexible state. In both instances, however, the form of the bone is perfectly preserved, showing how intimate must be the connection between the organic and inorganic constituents. The spongy flat bones contain from 12 to 30 per cent. of water, the compact tissue from 3 to 7 per cent. The chemical analysis of dried bone shows that it consists of from 30 to 34 per cent. of animal matter, which on boiling yields gelatine, and from 66 to 70 per cent. of mineral matter, of which about 57 parts are composed of calcium phosphate, 8 parts of calcium carbonate, 1 part of calcium fluoride, and 1 part of magnesium phosphate.* The degree of hardness of bone does not altogether depend, as shown by the experiments of Dr. Stark,† on the proportion of

* For further details, and for the per-centage composition of the Ashes of Bones and Teeth, see Aeby, "Centralblatt," 1871, p 561; 1873, p. 97.

† "Edinburgh Medical and Surgical Journal," April, 1845.

mineral deposit they may contain; for the flexible, semi-transparent, easily-divided bones of fish contain as large a proportion of earthy matter as the ivory-like leg bones of the deer or sheep. As a general rule, the bones of the extremities contain more calcium carbonate and phosphate than those of the trunk, and the larger long bones more than the smaller ones.* There is no difference in the composition of the corresponding bones of the two sides of the body,† and within certain limits (20—80) age has little or no influence upon it. It is also but very slightly influenced either by the proportion or the nature of the salts contained in the food.‡ It is very tough and elastic. The power of resisting pressure possessed by bone is very great, being nearly three times more than elm or ash, and twice as much as box, yew, or oak.§ The weight of the skeleton is to that of the whole body about as 10·5 : 100 in man, and as 8·5 : 100 in woman. The specific gravity of bone varies from 1·898 to 1·964. The natural process of absorption which parts of various bones and the fangs of the first set of teeth undergo is effected by means of multinucleated cells, to which Kölliker‖ has recently applied the term 'osteoclasts' or 'osteophagous' cells. These present a fimbriated border on that part of the cell which is turned towards the bone undergoing absorption, and it is by their action that all foramina, canals, and grooves in bone are produced. In the long bones of Man and of most Mammalia, the central cavity, which may be considered as an enlarged Haversian canal, is filled with the fatty matter known as *marrow*. This substance differs from ordinary adipose tissue in the nearly complete absence of connective tissue, the cells being supported by the spiculæ and lamellæ of bone which project into the cavity of the shaft. It is composed of 96 parts of fat, 3 parts of fluid, and 1 part of connective tissue. It has been shown to contain lymphoid corpuscles which have no nucleus, but are capable of performing amœboid movements, and are sometimes named 'medullary-' or 'medullo-cells.' With these are large spheroidal cells, presenting one or more nodular or tuberculated nuclei,¶ and large cells with many nuclei.** Although Neumann†† and Bizzozero‡‡ have observed some lymphoid corpuscles in bone which have a reddish tinge, and possess a nucleus, the observations of Hayem§§ do not support the view that these bodies are in process of development into red blood corpuscles, or that the cancellous tissue of bones is an hæmatopoietic organ. Ranvier even‖‖ thinks the coloration of these cells is due to yellowish or brownish granulations, which are the remains of red blood corpuscles that have undergone disintegration, and are in process of removal. In the cancellous tissue forming the expanded extremities of the long bones, and in the bodies of the vertebræ and of the carpal and tarsal bones, a peculiar reddish fluid is found, to which the term marrow has incorrectly been applied, since it contains only a trace of fat. Its per-centage composition is—water 75 parts; albumin, fibrin, and salts, 25 parts. Bones are but feebly supplied with sensibility. A few small nerves may, however,

* Fossil bones sometimes contain a very large amount of Calcium fluoride. Lassaigne, for example, found 15 per cent. in a tooth of the Anoplotherium.

† Aeby, "Centralblatt," 1871, p. 561.

‡ See "Weiske Zeits. f. Biologie," Band vii. pp. 179 and 333, viii. 239, and ix. 541; and Papillon, "Robin's Journal de l'Anat.," t. vi. 153. Heitzmann ("Wien. Anzeig.," 1873, p. 113) shows that either feeding with, or subcutaneous injection of, lactic acid produces Rachitis and Osteo-malacia in Carnivora. § Robinson, in *Lancet*, 1846, vol. i. p. 346.

‖ "Verhandlung: der Wurzbürger Physik und Gesellschaft," N. F. Band ii. 1872.

¶ The 'cellules à noyaux bourgeonnants' of Bizzozero. See his Essay, 'Sul midollo delle osse,' Napoli, 1869, p. 11.

** The 'Myeloplaxes' of Robin, "Comptes Rendus de la Société de Biologie," 1849, p. 119.

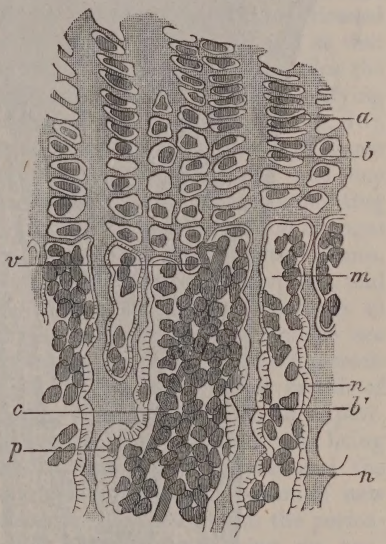
†† "Centralblatt für die Med. Wiss," 1868, p. 689. ‡‡ Loc. cit., p. 13.

§§ "Le Progrés Medical" March 29, 1879. ‖‖ "Traité d'Histologie," p. 324, 1875.

be seen to enter the shafts of the long bones with their nutritious arteries, and to be distributed in the endosteum.

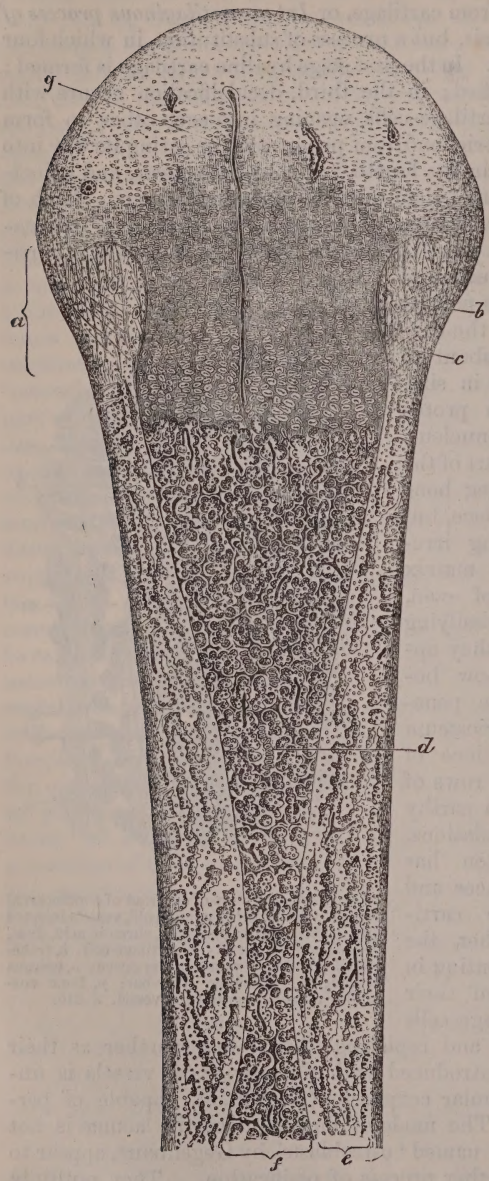
51. The development of bone from cartilage, or *Intra-cartilaginous process of ossification*, is not a metamorphosis, but a process of substitution, in which four distinct stages may be recognised. In the first stage hyaline cartilage is formed; in the second, it becomes calcified; in the third, decalcification occurs with absorption of the tissue, the cartilage-cells opening into each other to form large spaces, and the vascular perichondrium penetrating or eating its way into the non-vascular cartilage; and in the fourth, 'osteoblasts' appear, and coincidently the true or permanent bone is laid down in successive layers. Each of these stages requires a brief description. Just before the process of ossification commences in such a long bone as the femur, it is found to consist of cartilage invested by a layer of fibrous tissue which subsequently becomes the periosteum. In the central part of the cartilage when the ossification is about to commence the capsules increase in size, and are completely filled with protoplasm containing a vesicular nucleus. (See Fig. 39, *a*, and the central part of the cartilage of the head of the long bone in Fig. 40.) Proliferation takes place, but the new cells instead of being irregularly distributed through the matrix form long rows (*a*) like piles of coin, arranged perpendicularly to the ossifying point, and becoming larger as they approximate it. The cartilage now becomes softer, and begins to be penetrated by processes of the periosteum carrying bloodvessels the portions of cartilage intervening beween the rows of cells becoming impregnated with earthy salts in the form of minute granulations. When this deposit or infiltration has taken place absorption commences and the cavities occupied by the cartilage-cells open into one another, the newly-formed larger spaces presenting in their festooned borders traces of their mode of origin. The cartilage-cells have by this time disappeared, and replacing them—but whether as their descendants, or as newcomers introduced with the periosteal vessels is unknown—are small polygonal granular corpuscles (Fig. 39, *c*), capable of performing amœboid movements. The mode of formation of the lacunæ is not certainly known. These bodies, named 'osteoblasts' by Gegenbaur, appear to play an important part in the further process of ossification. They multiply and form a continuous investment to the inner surface of the medullary cavities, and around and beneath them the first lamella of true bone is developed. The newly-formed bone, which is thicker as it is more remote from the cartilage, at length encloses some of the osteoblasts, which probably become the bone corpuscles, occupying the lacunæ of the mature bone (Fig. 39, *p*), but as the osteoblasts that are buried in the newly-deposited bony lamellæ

Fig. 39.



Longitudinal section of the head of a metacarpal bone of a rabbit three months old, vessels injected with bichromate of ammonia, chromic acid, gum, alcohol, and purpurin.—*a*, cartilage-cell; *b*, trabecula of cartilage; *m*, medullary space; *n*, osseous festoon; *b'*, directing cross-bar; *p*, bone corpuscle; *c*, medullary cell; *v*, vessel. × 210.

Fig. 40.



present in many instances a stellate form, it is reasonable to think that they constitute the lacunæ. The canaliculi, it is suggested by Ranvier, are spaces or fissures left between two festooned borders of bone, as this gradually advances upon the protoplasm of the osteoblast. The primary osseous lamellæ are deposited on the partially absorbed and partly calcified cartilaginous trabeculæ, which run for the most part parallel to the axis of the bone, and have been named 'directing trabeculæ' by Ranvier.* The central cells remain as the medulla.

52. Ossification, instead of taking place in cartilage, may occur in connective tissue, and to this form the term 'intra-membranous' is applied to distinguish it from the 'intra-cartilaginous' form, which has just been described. It is best seen in the flat bones forming the vault of the cranium, but is also the mode in which the long bones increase in girth. In such a bone

Section through the middle of the humerus of a fœtal sheep. The entire bone was about one inch long—*f*, the part of the shaft which was primarily ossified in cartilage; what remains of the primary bone is represented dark and enveloped by the clearer secondary deposit. The areolæ of this bone are occupied by osteoblasts, with bloodvessels variously cut and represented as dark lines. One long straight vessel, *g*, passes in advance of the line of ossification, far into the cartilaginous head, most of the others loop round close to the cartilage. At one or two places in the older parts of the bone (*d*) elongated groups of cartilage-cells may still be seen, which have hitherto escaped absorption. The part of the bone that has been ossified in membrane, that is to say, in the osteoblastic tissue under the periosteum, is seen at *e*. It is well marked off from the central portion, and is bounded peripherally by a jagged edge, the projections of which are indistinctly seen to be prolonged by branches of osteogenic fibres. A row of osteoblasts covers the superficial layer of the bone. The subperiosteal layer is prolonged above into the thickenlng, *a*, which lies in a groove termed by Ranvier the '*encoche d'ossification*,' and which encroaches upon the cartilage of the head of the bone. In this are seen amongst numerous osteoblasts and a few bloodvessels the straight longitudinal osteogenic fibres, *b*, and some other fibres, *c*, crossing their direction and probably representing the perforating fibres of Sharpey. After Schäfer, partly diagrammatic, magnified about 30 diameters.

* Dr. Ogston remarks that in bone formed from cartilage the chief trabeculæ run at right angles to the plane of the bone surface, whilst in periosteal cartilage they run parallel to the surface, or have no definite direction. ("Journal of Anat. and Phys.," vol. xii. p. 505.)

as the parietal, a deposit of calcareous matter takes place at one point and forms a centre, from which irregular pointed processes radiate into the adjoining connective tissue. Schäfer* describes the spiculæ as terminating in fasciculi of nearly straight stiff-looking osteogenic fibres, between which lie numerous osteoblasts. The calcareous deposit gradually extends into the fibres and intermediate osteogenic substance, and forms the first lamella of the new bone. New osteogenic fibres shoot out from numerous points, and interlacing form a layer, in which again fresh osteoblasts and osteogenic substance appear, with deposit of calcareous matter; and thus a succession of lamellæ are developed by which the bone is thickened, larger channels being left, constituting the Haversian canals, and occupied by vessels and smaller spaces which are the lacunæ. The subperiosteal ossification of the long bones is the same as that of the membrane bones of the skull. The calcareous deposit occurs in the deeper part of the periosteal membrane, and fresh layers are constantly being added by which the girth of the bone is increased. At either end of the shaft the periosteal bone is prolonged for a little distance over the surface of the cartilage, so that the formation of the periosteal membrane bone always slightly precedes the extension of the cartilage bone within. This advanced part of the ossifying cartilage occupies a groove on the surface of the cartilage (as shown in Fig. 40), and is composed of osteoblasts and straight tapering fibres, or osteogenic fibres (*b*), which become the reticulating fibres of the perfect bone; and they are crossed by others (*c*), which probably subsequently become the perforating fibres of Sharpey. Even after the completion of the bone, interstitial changes are continually taking place in its substance, as in that of the softer tissues, old Haversian systems being partially, or entirely removed by absorption, and new ones being developed in their place. And it is to the persistence of portions of these older Haversian systems that the intermediary lamellæ are due. The clavicle and lower jaw are the first bones to ossify, their osseous centres or points of ossification appearing at the close of the first month of fœtal life. Increase in the length of a bone—as may be shown in experiments made by feeding an animal with madder, the newly-formed bone being deeply tinged—takes place almost entirely between the epiphyses and the shaft; but probably also results in part from the interstitial deposition of new material;† increase in girth, by ossification immediately beneath the periosteum; absorption from within and deposition from without going on continually. The former takes place by intra-cartilaginous or '*endosteal*,' the latter by intra-membranous or '*ectosteal*' ossification.

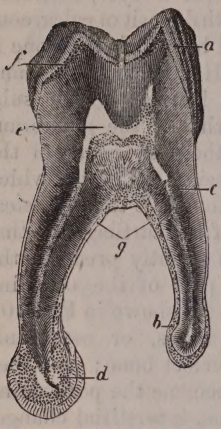
53. Teeth.—As soon as solid food is introduced into the mouth it is divided and comminuted by the Teeth. Partly in accordance with the general fact that epithelial growths die and are cast off to be replaced by others formed beneath them, but chiefly to allow for that enlargement of the jaws which occurs in the passage from infancy to adult age, two sets of these organs are developed—the first, temporary or milk teeth, which last up to the seventh or eighth year, are 20, the second, or permanent set, are 32 in number. Both are firmly embedded in sockets or alveoli of the upper and lower jaws. The front or incisive teeth (8 in number) are, as their name implies, provided with a cutting edge for the prehension and division of morsels of food of appropriate size for mastication. The sharp-pointed canines (4 in number) pierce and cut the firmer and tougher constituents of our

* "Quart. Journ. of Microscop. Sci.," 1878, p. 139, and Pl. viii. Fig. 2.

† For arguments for and against the latter point see "Wolff. Cbl.," 1869, p. 849; 1870, p. 641; Volkmann in "Centralblatt," 1870, p. 129; Lieberkühn, "Centralblatt," 1872, p. 420; Ranvier, "Comptes Rendus," 1873, t. 77, p. 1105.

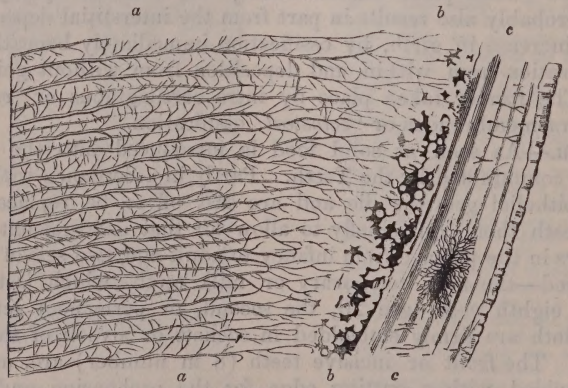
ordinary aliment, whilst the bicuspids (8) and the molars (12) triturate and bruise the food, till, with the aid of the saliva, it is reduced to the consistence of pulp; it is then fitted for deglutition. Every tooth consists of a crown, a neck, and one or more fangs (Fig. 41), and in all teeth three structures are found—the dentine, which gives the general form and size to the tooth; the enamel, which caps the crown; and the crusta petrosa, which invests the fang. On examining a thin longitudinal section of a tooth the *dentine* is found, like the shaft of the long bones, to be hollowed out into a pulp-cavity, containing a little connective tissue, with bloodvessels and nerves. These enter by a minute orifice at the extremity of the fang. The dentine which surrounds the pulp-cavity is composed of a matrix, which is traversed by numerous tubuli, that radiate from the pulp-cavity towards the external surface of the tooth, and which pursue a gently undulating course, dividing dichotomously, and sending off minute branches. In dry sections the tubuli, having a diameter of about 1-4500th of an inch, are seen to open into the pulp-cavity by one extremity, and by the other to terminate either by exquisitely fine branches, or in similar cavities in the dentine, or overstepping the limits of this, to end in the enamel, or crusta petrosa. The tubuli are most closely set near the crown of the tooth. In the living state they are occupied by prolongations of the protoplasmic cells which fill the pulp-cavity. These processes are not in direct contact with the matrix, but are invested by sheaths—the dentinal sheaths of Neumann. The *matrix* intervening between the tubuli is clear and homogeneous, and in softened specimens gives evidence of being deposited in lamellæ, concentric

Fig. 41.



Vertical section of *Human Molar Tooth*.—*a*, enamel; *b*, *g*, cementum or crusta petrosa; *c*, dentine or ivory; *d*, osseous excrescence, arising from hypertrophy of cementum; *e*, cavity, subsequently filled with osteodentine; *f*, osseous lacunæ at outer part of dentine.

Fig. 42.

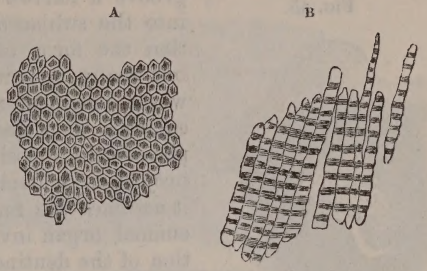


Section through the fang of a *Molar Tooth*.—*a*, *a*, dentine traversed by its tubuli; *b*, *b*, nodular layer; *c*, *c*, cementum.

with the pulp-cavity (Sharpey). Near the outer surface of the dentine, and also forming certain arched *contour lines* at the crown of the tooth, is a peculiar modification of the matrix, which appears to be broken up into spaces bounded by globular masses perforated with dentinal tubuli—the so-called interglobular layer. The *enamel* (Fig. 43) is composed of solid

four- or five-sided hexagonal prisms of about the 1-500th of an inch in diameter, arranged vertically to the dentinal surface on which they rest, and firmly adherent to one another. The course of these prisms is generally wavy, and their surfaces, in section, are marked by transverse striæ. Enamel is the hardest of all the tissues of the body, and is about equal to that of the mineral named apatite, which it resembles in hardness, crystalline form, and optical characters. As it possesses neither nerves nor bloodvessels, it is not liable to disease; but if from sudden alterations of temperature or from shocks it becomes fissured, particles of food, and perhaps bacteria and other low organisms, penetrate to the dentine, and cause its decay. Care should therefore be taken to brush the teeth after every meal, and to avoid very hot, cold, or acid food. The *crusta petrosa*, or *cementum*, corresponds in all essential particulars with the bone, possessing its characteristic lacunæ and canaliculi. It is destitute, however, of any lamellar structure. It is thickest at the extremity of the fang, and becomes gradually thinner towards the neck of the tooth, where it terminates. The following are the results of Von Bibra's analysis of the component structures of human teeth:—

Fig. 43.



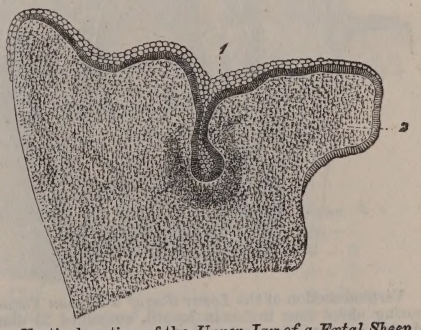
A, Transverse section of *Enamel*, showing the hexagonal form of its prisms; B, separated prisms.

Incisors of Adult Man.

	Dentine.		Enamel.		Cementum.
Organic matter	28·70	...	3·59	...	29·27
Earthy matter	71·30	...	96·41	...	70·73
	100·00		100·00		100·00

Hoppe-Seyler* assigns the following per-centage composition to the enamel of the new-born child:—$Ca_{10}CO_3,6(PO_4)$, 82·40; $CaCl_2$, 0·23; $MgHPO_4$, 2·37; soluble salts, 0·35; organic substances, 15·59; whilst to the dentine he gives the formula, based on Aeby's analyses, of $Ca_{10}CO_3 6(PO_4)$, 72·06; $MgHPO_4$, 0·75; organic substances, 27·70 = 100·51.

Fig. 44.



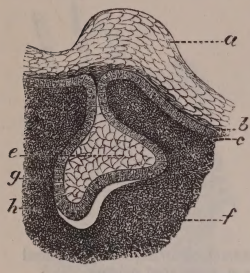
Vertical section of the *Upper Jaw of a Fœtal Sheep*, about 2 inches long, showing the enamel germ, with the semilunar rudiments of the dentine germ and dental sac in transverse section. 1, Dental groove; 2, Palatal process, magnified 50 diam.

In tracing the *development* of the teeth they are found to be essentially dermal structures, which have undergone calcification, the epithelium forming the enamel, and the mucous tissue the dentine and cement. At the sixth week of fœtal life a deep narrow groove may be perceived in the upper jaw of the human embryo, between the lip and the rudimentary palate. This is speedily divided into two by a ridge, which afterwards becomes the external alveolar process; and it is in the inner groove, which is termed the *primitive dental groove*, and is formed

* "Physiolog. Chemie," 1878, p. 182.

exclusively by a depression of the Malpighian layer, that the germs of the teeth subsequently appear. The groove is at first completely covered as well as filled with the thickened epithelium of the oral cavity, so that on a surface view it is scarcely perceptible. From the bottom of the dental groove a narrow process of the oral epithelium dips into the subjacent mucous tissue, presenting on section the form of a short tubular gland (Fig. 44), but really constituting an epithelial fold along the whole length of the jaw. As this fold deepens and enlarges a projection of the mucous tissue takes place in the opposite direction (Fig. 45, *f*, 46, 5). This projection or papilla is the *tooth germ*. By its growth it assumes the form of a club-shaped mass, and the enamel organ invests it like a cap. The first formation of the dentine is effected by cells, termed *odontoblasts*, which lie in the delicate connective tissue, near the surface of the papilla. The odontoblasts arrange themselves vertically to the surface, and each sends forth a process towards the enamel organ (Fig. 47 *a*), around which a dentinal tubule is secreted. They present occasional divisions.

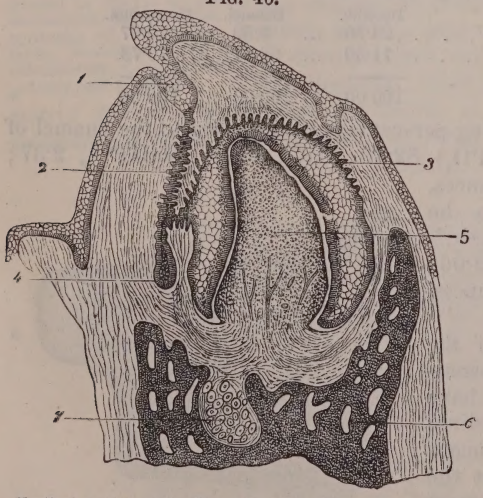
Fig. 45.



a, Epithelium.
b, Younger layer of the Epithelium.
c, Inferior layer of the Epithelium.
e, Enamel organ.
f, Dentine germ or papilla.
g and *h*, Inner and outer layers of the sacculus that is about to form.

Between the papilla or tooth germ and the connective tissue forming the wall of the sacculus is seen a spongy tissue (3) composed of cells, which forms the *enamel organ*. The innermost layer of cells, which are in immediate contact with the papilla, are columnar and regularly hexagonal in section. Their extremities are destitute of a cell-wall, though elsewhere it is well defined. Near the base of the papilla the cells become more cubical, and are reflected at its base upon the inner surface of the wall of the sacculus. The polygonal cells intervening between these two layers become stellate and anastomose with each other, the interspaces being filled with a gelatinous substance, which appears to form a kind of pabulum for the growth of the columnar enamel cells. At all events, it undergoes atrophy, so that the outer and inner epithelial layers come into close apposition; and in teeth examined just at the period of eruption a membrane can be detached from the enamel, composed of one or more layers of very flat epithelial cells, which Waldeyer entertains no doubt represent the cuticle, with more or less of the stratum intermedium or rete mucosum. The enamel itself proceeds from the

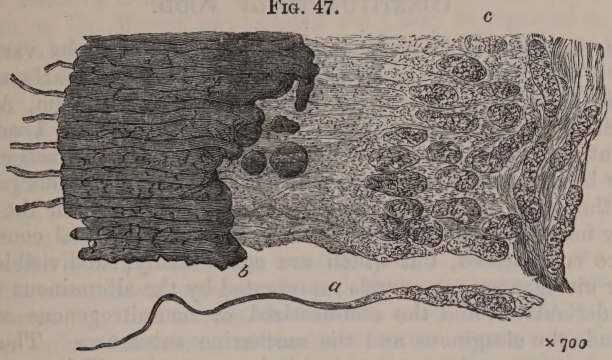
Fig. 46.



Vertical section of the *Lower Jaw of a Human Fœtus*, measuring about four inches in length, magnified 25 diam.—1, dental groove; 2, remains of the enamel germ; 3, enamel organ, presenting epithelium on both its outer and inner surface—*i.e.*, where it lines the sacculus and where it covers the papilla; 4, enamel germ of the permanent tooth; 5, papilla; 6, section of inferior maxilla; 7, Meckel's cartilage. The dental sacculus will be observed to present a number of fine papillæ opposite the dental papillæ.

direct calcification of the long columnar cells, the deposition of the calcareous salts taking place with tolerable uniformity in their outer ends. When the calcification has proceeded to a certain extent, the calcified part may be raised

Fig. 47.



Thin section of the inner portion of the *Dentine*, and of the surface of the Pulp, of an adult Incisor Tooth.—*a*, portion in which calcification is complete, showing separate globular masses at the line of junction with the uncalcified substance, *b*; at *c*, odontoblasts.

in the form of a membrane (Raschkow's 'membrana preformativa'), from the subjacent softer tissue; and thus, as Huxley first demonstrated, the enamel is a petrified epithelium. The formation of the *cement* is identical with the process of intra-membranous ossification in bone. The matrix of the cement is the loose mucous connective tissue of the dental alveoli immediately surrounding the teeth.* As early as the fifth month, before the calcification of the primitive pulps commences, a provision is made for the production of the 'permanent' teeth, the capsules of which originate in buds or offsets from the upper part of the capsules of the 'temporary' or milk teeth. These offsets are at first in the condition of open follicles communicating with the cavity of the primitive tooth; but they are gradually closed in, and detached altogether from the capsules of the milk teeth forming the *reserve sacs*. The three permanent molars, which are superadded in the adult to the milk teeth of the infant, are produced by a precisely similar process of budding from the reserve sac detached from that of the last milk molar.

The following are the principal dates connected with the development and eruption of the teeth:—

Temporary or deciduous teeth.		Permanent teeth.
Period of formation of papilla.	Period of eruption.	Period of eruption.
Week of intra-uterine life.	Month after birth.	Years.
Anterior molars . 7th	Cent. incisors . 7th	First molars . . . 6½– 7
Canines . . . 8th	Lat. incisors 8–10th	Central incisors . . 7 – 8
Central incisors . 9th	Ant. molars . 12–13th	Lateral incisors . . 8 – 9
Lateral incisors . 9th	Canines . . 14–20th	First bicuspids. . . 9 –10
Posterior molars 10th	Post. molars 18–36th	Second bicuspids . . 10 –11
		Canines . . . . . 12 –12½
		Second molars . . . 12½–14
		Third molars . . . 16 –30

* For a full account of the structure and development of the teeth, see Waldeyer's Essay in Stricker's "Human and Comparative Histology," 1870; Syd. Soc. Trans., vol. i. p. 463, to which an excellent bibliography is attached. Also Quain and Sharpey, 8th edit., vol. ii., p. 313. Wenzel, Pamphlet, Leipzig, 1871. For the resorption of parts of the teeth see Kölliker, "Centralblatt," 1872, pp. 353 and 369.

CHAPTER IV.

CHEMICAL COMPOSITION OF THE BODY AND OF THE CHIEF CONSTITUENTS OF FOOD.

54. The elements which enter into the composition of the various fluids and solids of the body are Oxygen, Hydrogen, Nitrogen, Carbon, Sulphur, Phosphorus, Chlorine, Fluorine, Potassium, Sodium, Lithium, Aluminium, Calcium, Silicon, Magnesium, Manganese, Copper, and Iron. Lead is occasionally, but perhaps only accidentally, present.* The combinations of these elementary bodies are divisible into two great groups: the Inorganic represented by the saline constituents, in which they are united for the most part in a binary manner, and the Organic, in which the chemical constitution is much more complicated, but which are again easily subdivisible into the azotized or nitrogenous compounds represented by the albuminous substances and their derivatives, and the non-azotized or non-nitrogenous compounds, which include the oleaginous and the saccharine substances. The inorganic compounds are commonly associated with the organic in sufficient quantities to maintain the body in health, if the food be sufficiently varied, though in one or two instances—as in those of the use of water and of common salt—an additional supply is taken in the pure state. The organic group is primarily and entirely derived from Plants, the office of which is to produce, from the surrounding air, water, and soil, the complex materials of which the bodies of animals are constructed. The inorganic compounds undergo comparatively little change in passing through the body, but the organic—and especially those belonging to the azotized or albuminous type, which have a complicated constitution, their molecules being larger and containing many atoms held together by comparatively feeble affinity—are correspondingly liable to break down under the influence of disintegrating causes, and by their oxidation to liberate the various forms of force which the animal body exhibits. If, for instance, we follow the changes undergone by the albuminous group we shall find that they no sooner enter the stomach than they are placed under conditions—namely, warmth and moisture—that are particularly favourable to decomposition. The peculiar properties of the gastric juice, however, retard and, at the same time, modify the changes they would otherwise undergo. By rendering them soluble it enables them to be absorbed into the blood where they are exposed to the action of oxygen, in a very active state, dissolved in an alkaline fluid. A portion is probably immediately applied to the maintenance and reconstruction of the tissues, and to the formation of the albuminoid constituents of the various secretions, which, in the form of Mucin, Collagen, Spermatin, &c., may be regarded as the immediate derivatives of albumin, whilst a part remains in solution in the blood, and forms a reserve store. Both portions alike—that which forms part of the tissues, and that which forms part of the blood—sooner or later unite with oxygen, and appear to break up into two groups of compounds, the azotized and the non-azotized. The former include such substances as Leucin, Glycin, and Taurin; the Biliary and Urinary acids, Kreatin, Kreatinin, and Urea; and the nitrogenous pigmentary substances. The latter—or non-nitrogenous group—are divisible into those which contain less oxygen than the albuminous compounds, as the fats; or more oxygen, as the carbo-hydrates, glycogen, milk, sugar, and the like. The ultimate results of the further oxidation of

* See Blasius, "Zeits. f. Rat. Med.," Band xxvi. p. 250; and Lossen, "Journal f. Chemie," 1866, p. 460.

both classes of compounds are carbonic acid and water.* The fats and carbohydrates ingested into the stomach, after some preparatory processes, are absorbed into the blood, and undergo the same changes as the corresponding compounds resulting from the breaking up of albumin and its allies. The tissues again, as Dr. Marcet has pointed out,† may be regarded as formed of three different classes of substances—namely, those which constitute the mature or functionally active tissue, and are characterized by being insoluble in water; next, those on their way to form the living tissue—which are soluble in water but of colloidal nature, *i.e.*, incapable of diffusion; and, finally, those which, having performed their function, are effete, and are on the road to be eliminated. These are soluble in water and are crystalloid. Considerable practical difficulty, however, exists in determining whether a particular substance belongs to one class or the other, and in the following account of the proximate principles entering into the composition of the body, we shall first describe the albuminous compounds and their derivatives; secondly, the hydro-carbonaceous; and thirdly, the mineral compounds, following as far as possible that order of descent from the higher to the lower planes of complexity of constitution which experiment and observation render probable.

55. Albuminous Compounds.‡—The albuminous compounds which enter so largely into the composition of the bodies of animals are entirely derived from plants. These yield them to the Herbivora, which are again consumed by the Carnivora. They all contain Carbon, Hydrogen, Nitrogen, and Oxygen, and Sulphur is usually, but not invariably, present. Phosphorus, though often considered to enter into their composition, is now believed to result from contamination with mineral phosphates or with lecithin.§ The grouping of the atoms is so complex that it is difficult to represent it by any rational formula. That of Conglutin obtained from almonds has been given as C_5H_5NO; of Legumin from peas, as $C_{33}H_{54}N_{10}O_{11}$; and of the Fibrin of maize, as $C_{37}H_{59}N_{10}O_{11}$.‖ A knowledge of their per-centage composition is more easily attained, and the subjoined Table¶ will show the close similarity in the composition of those that have been most carefully examined. All the forms of albumin are very unstable, and not only easily decompose themselves, but in decomposing act as excitors of fermentation in other bodies. Most of them exist in two states—a soluble, and an insoluble. The former may be obtained by evaporating the fluids in which they are contained below 100° C. to dryness, when the albuminous substance appears as an amorphous semi-

* The successive steps may be traced, perhaps, most distinctly in the case of guanin ($C_5H_5N_5O$), which is a constituent of the pancreas, through hypoxanthin ($C_5H_4N_4O$) and xanthin ($C_5H_4N_4O$) to uric acid ($C_5H_4N_4O_3$); uric acid again, when acted on by oxidizing agents, yielding urea (CH_4N_2O), allantoin ($C_4H_6N_4O_3$), oxalic acid ($C_2H_2O_4$)$_2$, and carbonic acid (CO_2).

† "An Experimental Enquiry into the Nutrition of the Animal Tissue," 1874.

‡ The best complete accounts of the albuminous compounds are to be found in Von Gorup Besanez, "Lehrbuch der physiologischen Chemie," 1874; Karl Hofmann, "Lehrbuch der Zoochemie," 1879; Hoppe-Seyler, "Physiologische Chemie," 1878; and Kingzett, "Animal Chemistry," 1878; but many scattered papers appear in Pflüger's "Archiv," and the "Zeitschrift f. Chemie," 1876, 1877, and 1878. See also Brunton and Power, "St. Bartholomew's Hospital Reports," vol. xiii. p. 283.

§ Kingzett, "Animal Chemistry," 1878, p. 359.

‖ Settegast, Pflüger's "Archiv," Band xvi. 1878, p. 293.

¶

	Pure egg-albumin.	Serum-albumin.	Fibrin.	Syntonin.	Globulin.	Casein.
C	... 52·9 –54·7	... 53·5	... 52·6	... 54·1	... 54·5	... 53·3
H	... 7·01 – 7·7	... 7·0	... 7·0	... 7·3	... 6·9	... 7·1
N	... 15·6 –15·8	... 15·5	... 17·4	... 16·0	... 16·5	... 15·7
O	...24·49 –21·8	... 22·4	... 21·8	... 21·5	... 20·9	... 22·6
S	... —	... 1·6	... 1·2	... 1·1	... 1·2	... 1·0

transparent yellowish material, resembling gum arabic, free from taste and smell, neutral to test-paper, and with the exception of Hæmoglobin, quite destitute of any tendency to crystallize. The insoluble form is obtained by heat or by precipitation with various chemical reagents, and forms whitish flocculent masses, which present a granular aspect under the microscope. The albuminous compounds belong to the group of Colloids, founded by Professor Graham, which possess an extremely low power of diffusion through animal membranes. To this peculiarity their feeble taste may in all probability be attributed. They have little or no smell. They dissolve in concentrated acetic and phosphoric acids, and with partial decomposition in caustic alkalies. They are precipitated by alcohol, ether, tannic acid, corrosive sublimate, and most of the mineral acids. On the application of nitric acid they become yellow; concentrated boiling nitric acid dissolves them, forming a yellowish solution which becomes orange on the addition of ammonia (xanthoproteic test); concentrated hydrochloric acid dissolves them, the solution assuming a blue colour. They are precipitated by potassium ferrocyanide. Solution of iodine stains them of a yellow colour, and they all become red at 212° F. when acted on by Millon's reagent, which consists of a solution of the proto- and per-nitrate of mercury. Sulphuric acid holding molybdic acid in solution stains them a dark blue (Frohde's reaction), and when treated with sugar and sulphuric acid under the microscope they give a beautiful violet colour (Schultze's reaction). Von Gorup Besanez* observes that when acted on by powerful oxidizing agents, the albuminous compounds yield formic, acetic, propionic, butyric, valerianic, caproic, and benzoic acids, the aldehydes of these acids, ammonia, and volatile bases; whilst by the action of acids, alkalies, and during putrefaction, they give rise to volatile fatty acids, leucin, tyrosin, glycin, ammonia, volatile bases, sulphide of ammonium and indol, a volatile crystallizable substance having the odour of fæces. In health no albumin is found in the bile, urine, sweat, or tears, though many of the products of the disintegration of albuminous substances can be extracted from those parts of the body, as the glands, in which active processes of metamorphosis are taking place. It is reasonable to suppose, therefore, that the successive stages undergone by the albuminous substances within the body are essentially similar to those through which they pass, when acted on by chemical agents without the body. The aqueous solutions of albumin rotate the plane of polarization to the left.

The albuminous compounds, as the following Table taken from the same author will show, are widely distributed through the body, and in fact may almost be said to be everywhere present.

In 1000 parts of—

Fluids	are of albumin	Tissues	are of albumin
Cerebro-spinal fluid	0·9	Spinal cord	74·9
Aqueous humour	1·4	Brain	86·3
Liquor amnii	7·0	Liver	117·4
Intestinal juice	9·5	Thymus (of calf)	122·9
Pericardial fluid	23·6	Egg (of fowl)	134·3
Lymph	24·6	Muscle	161·8
Pancreatic secretion	33·3	Middle coat of arteries	273·3
Synovia	39·1	Crystalline lens	383·
Milk	39·4		
Chyle	40·9		
Blood	195·6		

With the exception of Hæmoglobin, which is described in the section on

* "Phys. Chemie," 1874, pp. 39 and 117.

Blood, and Peptones in the section on Gastric Digestion, the chief albuminous compounds will be considered in the following order :—

Albumins	Egg albumin Serum albumin Muscle albumin Acid albumin Alkali albumin Casein
Globulins	Vegetable globulin Vegetable myosin Serum globulin.
Vitellins	Vegetable vitellin Animal vitellin

Ferments

Derivatives of albumin.

Egg Albumin—Ovalbumin—*Albumen—White of Egg.*—This Albumin is contained in meshes formed by a number of fine intersecting fibres. On whipping the white with water the albumin dissolves and the fibres are slowly deposited. The solution forms an opalescent, very slightly alkaline fluid, rotating the plane of polarization 35°·5 to the left, and coagulating completely at 75° C. (167° F.). There appear to be two different forms or kinds of albumin in the white of the egg of the bird—one coagulating at 63° C. (146° F.), and rotating the plane of polarized light $-43°$; the other coagulating at about 74° C. (165° F.), and rotating the plane $-26°$;* and there are some points of difference between the eggs of different birds. Ordinary white of egg contains about 12 per cent. of dry albumin. If it be dried *in vacuo* at ordinary temperatures, or below 50° C., ovalbumin may be heated to 100° C. without being rendered insoluble. It may be obtained so pure that it leaves when burnt no perceptible weight of ash.†

Serum Albumin—*Blood Albumin—Serin.*—The blood contains about 7 per cent. of a peculiar form of albumin, which is also found in lymph and chyle, in all serous fluids, and transudates; as in hydrocele fluid, in colostrum, and in very small quantity in the milk (Lactoprotein), in the fluid of the amnios, and is the common form in which albumin appears in the urine in cases of renal and cardiac disease. Its solutions become cloudy at 60° C., and coagulate at 72°—73° C. When pure it is soluble in water, insoluble in alcohol and ether, yet is not precipitated from its watery solution by ether. It is not precipitated by very dilute acids, by the alkaline carbonates, common salt, or platinum cyanide. Its rotatory power is $-56°$. When injected beneath the skin it does not appear in the urine, whilst ovalbumin is quickly eliminated unchanged. The addition of potash or soda converts it into Lieberkühn's alkali-albuminate.

Muscle Albumin—*Myosin.*—Pure myosin may be obtained by allowing the uncoagulated juice of muscle to fall into water. Each drop forms a gelatinous spheroid, and may then be washed with water. Myosin may also be prepared by kneading finely-minced muscle with water till all traces of blood are removed. It is then triturated with a mixture of one part of saturated solution of common salt and two parts of water; the fluid is filtered, and a frag-

* Gautier, "Bull. Soc. Chem.," 1870, t. xiv. p. 177.

† This may be accomplished by desiccation at a low heat; pulverization, digestion with water at 30° C. (86° F.); filtration, precipitation with alcohol, desiccation at 100 °C. (212° F.); and solution in water acidulated with a trace of acetic acid, which may be afterwards removed by dialysis. On final evaporation pure ovalbumin remains.

ment of rock salt added to it. As this dissolves the myosin is precipitated in flocculi, which may be purified from salt by washing with water. Moist myosin thus obtained dissolves easily in 10 per cent. solutions of common salt, but is no longer dissolves in them after desiccation *in vacuo*. The solution in 10 per cent. NaCl coagulates at 55°—60° C. (131°—140° F.). It is converted into syntonin by very dilute solutions of hydrochloric acid, and into alkali-albuminate by the caustic alkalies. It has the power of rapidly decomposing peroxide of hydrogen. Kühne considers that the condition of the muscles termed Rigor mortis is referable to the coagulation of the myosin they contain.

Acid Albumin—*Syntonin.*—Acid albumin is a product of the action of acetic or of strong hydrochloric acid on various forms of albumin. The term Syntonin is especially applied to the substance obtained by the action of dilute hydrochloric acid (1–1000) on myosin, and is synonymous with Meissner's parapeptone. On exact neutralization with sodium carbonate, a gelatinous mass is precipitated, which when purified from fat by ether is soluble in excess of the alkali, and in dilute acids and solutions of the alkaline carbonates, by which it is distinguished from fibrin, coagulated albumin, and amyloid, but not in solution of common salt, by which it is distinguished from the globulins. It is not precipitated by heat. When pure it is white, transparent, and gelatinous. It does not decompose ozone. Suspended in water at a temperature of 85° C. (185° F.) for a few minutes, syntonin undergoes a change, part of it becoming insoluble in water. Its lævo-rotatory power amounts to $-70°$ to $-74°$. Conversion into syntonin is the first change that albuminous substances undergo in gastric digestion.

Alkali-albumin, or Albuminate, is made by adding caustic potash to a solution of seralbumin or ovalbumin, and allowing it to stand for some hours. Its presence is detected by the precipitate which occurs on exact neutralization with an acid unless sodium phosphate be present, which distinguishes it from syntonin. Hoppe-Seyler obtains it by agitating milk with strong caustic soda and ether; removing the ethereal layer, and adding acetic acid to the watery layer, the precipitate is washed with water, cold alcohol, and ether. It contains no sulphur, the absence of which distinguishes it from casein. Its lævo-rotatory power on light is $-55°$. Its solutions are not precipitated on boiling. Its formula is given as $C_{72}H_{112}N_{18}O_{23}S$ (Hofmann). When placed in acid fluids it becomes opaque, and is converted into Brücke's Pseudofibrin. Acid albumin and alkali-albumin are grouped together under the term Protein by Hofmann.

Casein.—Olof Hammarsten* obtains casein by precipitating it from milk with a trace of acetic acid, dissolving it (after washing) in water containing a trace of alkali, filtering to separate the fat, precipitation with acetic acid; and after a repetition of these processes, frequent washing with alcohol and ether. The casein thus obtained has the character of an acid, giving, when moist, a distinct red stain to litmus-paper; dissolving in caustic alkalies, and expelling carbonic acid from the carbonates, whilst it dissolves the bases. It even dissolves calcium phosphate. The precipitate formed in solutions of casein by acids is by some regarded as a combination of the casein with the acid; but Hammarsten finds the whole of the acid may be removed by frequent washing with pure water. Casein varies in its solubility in different acid solutions—much more acetic than hydrochloric acid, for example, being required to precipitate it. The coagulation of casein by a peptic ferment only takes place when the solution contains a sufficient quantity of calcium phosphate or some other salt of calcium. In the act of coagulation casein splits into at least two new albuminous compounds, of which one, by far the most abundant, forms

* "Festschrift," &c., Upsala, 1877; and "Centralblatt," 1878, p. 470.

he cheesy substance precipitating with calcium phosphate, while the other is peptone-like substance which remains dissolved in the cloudy masses. Solutions of perfectly pure casein in caustic soda do not coagulate on the addition of rennet. One part of rennet ferment is capable of coagulating 800,000 parts of casein, and the addition of calcium chloride up to 0·5 per cent. hastens the process in a very remarkable degree. The casein of human milk is not precipitated on the addition of acids.

Globulin.—Under this term Hoppe-Seyler* includes all albuminous substances which are precipitated from their neutral solutions by the addition of a large quantity of water free from carbonic acid gas, and are completely soluble in dilute solutions of common salt and of neutral alkaline salts. When long in contact with water they gradually become insoluble in neutral solutions of common salt of any degree of concentration, and pass first into albuminate,† and subsequently into coagulated albumin (Syntonin). Acids and alkalies appear to produce the same effect with more or less rapidity. The different kinds of globulin are arranged by Weyl‡ into two groups, the animal and the vegetable, the former containing—(1) Vitellin, which is soluble in solutions of common salt of every degree of concentration; and (2) Myosin, fibrinogen and serum globulin or paraglobulin, which are all precipitable from their neutral solutions on the addition of a few crystals of common salt; and the latter containing vegetable vitellin, vegetable myosin, and vegetable casein. All forms of globulin, whether animal or vegetable, when in contact with water, acids, or alkalies, first pass into albuminates, and subsequently into coagulated albumin.

Vegetable Globulin.—This substance constitutes the albuminous basis common to almonds, peas, beans, lentils, and the cereals. Solutions of vegetable globulin in sodium chloride exhibit the same reactions as those of animal globulin and the animal albuminous compounds generally. They are precipitated by HNO_3, by dilute acetic acid, by acetic acid + potassium ferrocyanide, by acetic acid + sodium chloride, &c. They give a red colour with Millon's reagent, a violet colour on boiling with $KHO + CuSO_4$, &c. The coagula are insoluble in dilute acids and alkalies. The very dilute solutions of these bodies in NaCl are only partially precipitated by CO_2. The precipitate thrown down by H_2O from NaCl solutions dissolve at first completely in solutions of neutral alkaline salts, but after a time, if in contact with water, they change into albuminates, and then dissolve only in dilute hydrochloric acid and in one per-cent. solutions of soda. Vegetable globulin dissolved in a one per-cent. solution of Na_2CO_3 solution precipitated by $H_2 + CO_2$ and suspended in water by the addition of a few drops of a one per-cent. Na_2CO_3 solution, presents exactly the same characters as those of—

Vegetable Myosin.—This is a second globulin substance obtained by Weyl from a ten per-cent. salt solution of the albuminous compounds contained in wheat, peas, oats, white mustard, and sweet almonds. Like animal myosin, with which it agrees in all essential features, it coagulates at a temperature of 55°—60° C. (131°—140° F.).

Serum Globulin (*Weyl*)—*Fibrinoplastic substance*—*Fibrin ferment*—*Paraglobulin*—*Serum Casein* (*Kühne* and *Eichwald*)—*Globulin* (*Heynsius*).—This, according to Weyl, is the only globulin substance in the serum of blood. To obtain it pure, serum is diluted with 15 volumes of distilled water, and a few

* "Handbuch der Phys. Chemie," 1870, p. 196.

† The term albuminate here = alkali-albuminate + acid-albuminate = Protein of Soyka and Weyl.

‡ "Zeits. f. Phys. Chem.," Band i., 1878, p. 72.

drops of dilute acetic acid are added till the fluid is rendered neutral; a flocculent precipitate falls. This can be dissolved in a few drops of a ten per-cent solution of common salt, which takes up about 1·8 per cent. of it, and again precipitated by addition of water, and so on till pure. The clear neutral solution of serum globulin coagulates at 75° C. (167° F.). Serum globulin agrees in all its reactions with the myosin of transversely striated muscle, except that it coagulates at 20° C. (66° F.) higher temperature. The fibrinoplastic activity is greatest when it is obtained by precipitation with powdered salt.

Vitellin—*Vegetable Vitellin.*—This substance has been obtained in a crystalline form by Weyl from Brazil nuts, as well as from maize, peas, and other seeds, by the action of ether. It is the purest form of globulin known. Its elementary composition is C 52·43, H 7·12, N 18·1, SO·55, O 21·8, the proportion of nitrogen being thus extremely high. It coagulates at 75° C. (167° F.) when dissolved in a ten per-cent. solution of sodium chloride. Vitellin crystals are doubly refracting, and when long kept in contact with water a kind of Haptogen or precipitation membrane forms on their surface. These crystals correspond to the Aleuron crystals of Hartig.* Vegetable Vitellin agrees in all particulars with Animal Vitellin.

Animal Vitellin.—This is obtained by exhausting the yelk of egg with ether, which removing the coloured oil leaves vitellin with some lecithin and nuclein as a white residuum. This is dissolved in a very small quantity of a ten per-cent. solution of rock salt and precipitated with water, by a repetition of which process it is gradually purified. Its neutral clear solution in ten per-cent. solution of salt coagulates at 75° C. (167° F.). Substances which appear to agree in their reactions with vitellin have been found by Hoppe-Seyler in the chyle,† by Weyl in the amniotic fluid in a case of hydramnion at the seventh month, and by Hoppe-Seyler and Laptschinsky‡ in the lens of the ox.

Ferments, so far as is at present known, are of two kinds,§ the organized, particulate, formed, or insoluble, like yeast; and the unorganized, diffused, unformed, or soluble, like pepsin and ptyalin in the animal body, or diastase in the vegetable. The latter class of ferments are also called by Kühne Enzymes. We are as yet in total ignorance as to the rationale or method of working of ferments, and various theories have from time to time been put forward as to their mode of action. Of these the *contact theory* of Berzelius

* "Bot. Zeit.," 1855, p. 881; 1856, p. 263. "Entwickelungsgeschichte des Pflanzenkeimes," 1858, p. 108.

† See Weyl, loc. cit. p. 75, note.

‡ Pflüger's "Archiv," 1876, Bd. xiii. p. 633.

§ Hoppe-Seyler ("Physiologische Chemie," I. Theil, Berlin, Feb., 1877, pp. 113–122) classifies ferments into the two great divisions of organized (formed) and unorganized (unformed) ferments. The fermentative process he divides into—

I. A change from the anhydrous to the hydrated condition.
   a. The ferment acts like a dilute mineral acid at a boiling temperature: as in
      (1) The conversion of glycogen into dextrin and grape sugar.
      (2) The transformation of cane into grape sugar.
      (3) The change of benzole glucosides into sugar and simpler benzole derivatives.
      (4) The conversion of sulphur holding bodies into sugar, sulphuric acid, and oil of mustard.
   b. Ferments acting like caustic alkalies at a high temperature.
      (1) The conversion of ether, fats, &c., into alcohol and acids.
      (2) The decomposition of amide compounds under the influence of a putrefactive ferment by the taking up of water.
II. Fermentative changes with the transference of oxygen from hydrogen to carbon.
      (1) Lactic acid fermentation.
      (2) Alcoholic fermentation.
      (3) Putrefactive processes.

supposes that the ferments, chiefly the unorganized, possess a catalytic power, where is understood by the word catalytic the act of rearrangement of the molecules of a substance when the cause of the change is not itself changed; or, in other words, where the fermentation proceeds without causing corresponding changes in the ferment. The *mechanical theory* explains the action of ferments by supposing that they are substances whose molecules are in a state of rapid vibration; that these vibrations are communicated to the molecules of the substance in which fermentative changes are produced, but that the vibrations of the molecules in the two bodies being dissonant, those of the fermented body fall down or are rearranged, thereby producing new compounds, and at the same time liberating certain forms of energy. The *physical theory* of Willis and Stahl, advocated by Liebig, explains the phenomena of fermentation by supposing that "yeast, and in general all animal and vegetable matters in a state of putrefaction, will communicate to other bodies the condition of decomposition in which they are themselves placed, and the motion which is given to their own elements by the disturbance of equilibrium is also communicated to the elements of the bodies which come into contact with them."* Lastly, there is the *vitalist* theory, which has of late years received so much support from experiments carried out by Pasteur. This theory takes for granted that there are in the air numberless germs or spores of the lowest forms of plant and animal life; it is the germination of these spores in the fermenting substance which brings about those changes known as fermentative. Turpin sums up this theory in the formula, "Fermentation as effect, and vegetation as cause." As might be supposed, somewhat more is known about the organized than about the unorganized ferments. Taking, as an example of the former class, the yeast plant *Saccharomyces cerevisiæ*—a very low form of plant life—we find that it consists of a number of Plastids, or elementary organisms, aggregated into chains—the so-called Torula chains. These chains are, in the language of Herbert Spencer, feebly-pronounced indications of a secondary aggregate; they are formed by a process of exogenous gemmation. They grow very rapidly, if supplied with sufficient oxygen and proper food, and as they grow they set free large quantities of carbonic acid, whilst any grape-sugar which may be present is converted into alcohol. The growth of this Protophyte, therefore, brings about a certain change in a solution which contains grape-sugar—viz., the conversion of the grape-sugar or dextrose into ethyl alcohol, and it is this change which is known by the name of *alcoholic fermentation*. This fermentation is not dependent entirely upon the growth of the Saccharomyces, or any protophyte nearly allied to it; for the experiments of Pasteur† seem to prove that vegetable cells generally can produce alcohol and carbon dioxide at the expense of sugar; the action, however, is much less energetic than with yeast. In addition to the formation of alcohol and carbon dioxide, minute traces of other substances, such as succinic acid and glycerine, can generally be detected. This alcoholic fermentation is one of the simplest examples of fermentative action; chemically stated, it is roughly as follows: $C_6H_{12}O_6 = 2C_2H_6O + 2CO_2$. Dextrose, under the action of yeast, yields ethyl alcohol and carbon dioxide.

The means whereby this change takes place, and the mode in which it occurs, have given rise to the most diverse speculations. The theories on this subject may be divided into two classes, the chemical and the biological. In both cases the ferment as it grows is supposed to abstract something from the fermenting substance, and it is perhaps, on the whole, best to suppose that the

* Liebig, "Ann. de. Chem. et de Phys.," ser. ii. vol. lxxi. p. 178.
† "Comptes Rendus de l'Acad. de Sci.," vol. lxxv. p. 784, et seq.

phenomenon is fundamentally one belonging to biology and explicable upon biological grounds. In the first place it is to be remarked that the amount of yeast produced during a fermentation bears no relation to the amount of sugar which disappears, but is rather proportional to the amount of oxygen present.* Again, when yeast is deprived of sugar it undergoes a singular change, which appears to be due to its fermenting itself. In this case, as well as experiments with yeast which has been deprived of oxygen, it is found that the ferment action is reduced to a minimum ; but on the addition of a saccharine solution the action gradually increases and becomes stronger. From these and other considerations it appears best to suppose that the yeast contains within itself one of the second class of ferments, or a soluble ferment, and it has been actually found that an active solution of yeast, the so-called yeast-water, may be obtained, which is free from proteids. This yeast-water is rendered inactive by the addition of borax, a salt which has a neutralizing action upon the soluble ferments, though it does not interfere with the organized ferments.†

In the second kind of fermentation, due to the presence of an organized ferment, lactose or milk-sugar is converted into lactic acid. This change is known as *lactic acid fermentation ;* it has been supposed to be due to the presence of small globules formed of short joints, the lactic ferment, and this theory has been lately supported by Professor Lister,‡ who has given to the motionless protophyte, which brings about the change in milk known as souring, the name of Bacterium lactis.

A third organized ferment is that of the Mycoderma aceti, which effects the conversion of alcohol into vinegar—*the acetic fermentation* ; this same change can be brought about by subjecting alcohol to the action of spongy platinum, the great difference being that when platinum is used the alcohol is more readily transformed if it is concentrated, whereas with the Mycoderma the alcohol should not be more than 10 per cent. The action of the protophyte, however, is not simply mechanical, for the oxidizing property is lost above 95° F. and below 50° F.

The Butyric Acid Fermentation, in which lactic acid and all substances capable of undergoing lactic fermentation are made to yield butyric acid, is apparently due to a special form of Bacterium of the genus Vibrio;§ or, according to later researches, to bacillus. It is not yet known whether the alkaline fermentation which urine undergoes is due to an organized ferment,‖ or whether it is caused by the presence within itself of a peculiar soluble ferment which is capable of converting urea into carbonate of ammonium.¶

In considering the organized ferments, it is thus seen that they are divisible into two great groups : in the one fermentation is due to an order of protophytes known as the Saccharomyces, to which yeast belongs; in the other, the changes are brought about by another order of protophytes—the Schizomycetes; or, in simpler language, the fermentation is caused by the yeast-plant and its allies, or by Bacteria, of which there appear to be several forms. Yeast fermentation** requires oxygen in considerable quantities, and it forms products which are not disagreeable to the senses ; on the other hand, Bacteria fermentation does

* Pasteur, "Bullet. Soc. Chem.," 1861, p. 621.
† Dumas, "Comptes Rendus," lxxv. p. 295.
‡ "Quart. Journ. Micros. Sci.," April, 1878, p. 184.
§ Pasteur, "Comptes Rendus," lii. p. 344, Feb., 1861.
‖ C. Bastian, "Comptes Rendus," lxxxiii. No. 8.
¶ Musculus, "Comptes Rendus," lxxxii. p. 333.

** This appears, however, only to be the case with fresh yeast, for ready-formed yeast can grow in the absence of oxygen, the requisite oxygen being derived not from the sugar, but from albuminoid substances, since unaltered sugar is found in the liquid after the yeast has ceased to grow. When oxygen is excluded, yeast can induce fermentation in pure sugar solutions, but in this case the yeast does not increase. (Watts' "Dict. of Chemistry," vol. viii. part i., Supp. III., 1879, Art. Fermentation.)

not require oxygen, or at least it can obtain oxygen from the fermenting substance, and its products are very disgusting to the sense of smell. Witness many butyric fermentations; it is, in fact, putrefaction. It is very possible that in many artificial fermentations, and in some natural ones, as we have seen, Bacteria play a very great part, and that, too, in cases which are ordinarily supposed to be due to the action of a soluble ferment; though Hoppe-Seyler* states that there is a special ferment in Bacteria and others of the lowest organisms, which produces the processes of decay. This ferment he believes also to be present in the organs of higher animals, and probably also generally in plants. He bases his statement on the fact that the fermenting power is not lost when a watery solution is shaken up with ether and is then allowed to stand, although all living organisms are thereby destroyed. Heating to 53° C. destroys the ferment, which appears to be insoluble in water, or at any rate incapable of diffusion through animal membranes or dialyzing paper.

In the healthy animal body, so far as is at present known, *organized* or *particulate* ferments take no part, except perhaps doubtfully in the pancreas. The secretion of this gland, poured as it is into the alimentary tract, brings about a process of disintegration of proteid materials, which when carried to its furthest extent results in the formation of an unsavoury substance known as Indol. It is the presence of this material which gives to the excrementitious matter of the intestine, and to artificial pancreatic digestions, their peculiarly penetrating and unpleasant odour. Indol is always found to be produced concomitantly with a copious development of Bacteria in artificial digestions with pancreatic infusions; and as Bacteria are known to occur in the alimentary canal,† it is argued‡ that they have some influence in the production of Indol—that is to say, in carrying on the pancreatic digestion of albumins beyond its normal limit. Pathologically, organized ferments are found in the body. The disease known as malignant pustule in Man is caused by the growth of numberless small Bacterioid bodies in the blood. Dr. Cossar Ewart§ has studied the development of the Bacillus anthracis, whose relation to splenic fever was pointed out by Cohn and Koch.‖ Dr. Johnston¶ attributes Summer diarrhœa, such as ordinarily affects infants and adults in hot weather, to the presence in the intestine of Bacterium termo and the spherules of micrococcus which are found in large numbers in the stools and vomit of patients suffering from this disease. The Flacetodezza, or silkworm plague, is similarly due to the presence of Bacteria; whilst it has been put forward by some very competent authorities that syphilis and typhoid variola** are caused by the presence of organized ferments. These considerations, however, must be passed over, as they have already carried us too far from our present subject of ferments; and would lead us into the, at present, hotly-contested territory of contagia viva, or disease germs.††

Let us turn now our attention to the second class of ferments—*the Soluble Ferments.* From a physiological standpoint these ferments are of an even more absorbing interest than are the organized ferments, for they are primarily

* "Physiol. Chem.," th. i. p. 122. Berlin, 1871.

† Chiene and Ewart, "Journ. Anat. and Physiol.," vol. xii. 1878, p. 449.

‡ W. Kühne, "Unters. aus Phys. Inst.," Bd. i. heft 3; abstract in "Centralblatt f. Med. Wiss.," 1878, p. 357.

§ "Quart. Journ. Micros. Sci.," 1878, vol. xviii. p. 161.

‖ "Beitr. der Biol. der Pflänzen," Band ii. heft 2, 1876. See, however, for a different view on this subject, "An Appendix to the Fourteenth Annual Report of the Sanitary Commissioner with the Government of India, 1877," by Timothy R. Lewis, M.B.

¶ "The Lancet," 1878, p. 397. ** Von Feltz, "Comptes Rendus," lxxxv. p. 1288.

†† Parkes' "Practical Hygiene," 5th ed. p. 510.

the means whereby our food is digested, or converted into material fitted for assimilation by the tissues. As yet the nature and mode of action of unorganized ferments is absolutely unknown. We cannot tell whether they are one or many; whether they are all produced from a single substance, or whether each is formed by a peculiar body; whether they are secreted by special cells from the blood, or whether they are manufactured *de novo* in the gland itself; whether they are, after use, cast out of the body, or whether they are absorbed again into the circulatory medium. In dealing with the unorganized ferments it will be advisable to confine ourselves to those which are actually formed in the body. We shall therefore dismiss without further notice the ferment *Diastase*, which is found in malt, converting the starch present in the grain into dextrose or grape-sugar; *emulsin or synaptase*, which transforms amygdalin into oil of bitter almonds, hydrocyanic acid and glucose, and which acts generally upon glucosides; *Myrosin*, which converts potassium myronate into allyl, sulphocyanide, glucose, and potassium bisulphate; and finally, *Erythrozyme*, which splits up the glucosides found in madder-root which possesses the power of inducing alcoholic fermentation in solutions of sugar. In all these cases, as in soluble ferments generally, the process of fermentation is not hindered by the presence of oxygen, even at high pressures, whereas compressed oxygen destroys organized ferments after a longer or shorter time. Borax,* on the other hand, destroys all soluble ferments, whilst it has no effect upon the particulate ferments. By either of these methods, a particulate may be separated from a diffused ferment in any case of doubt. As yet no soluble ferment found in the animal body has been more than approximately isolated; perhaps Brücke's† extract of pepsin obtained by a complicated process, to be presently noticed, was the nearest approach to the isolation of a ferment of this description which has yet been made. This extract was active in the conversion of fibrin into peptone, but was itself free from all trace of proteids; it contained nitrogen. The general method for the approximate isolation of a non-particulate ferment may be thus indicated: the gland or mucous membrane from which the ferment is obtained is finely minced, and is then thrown into a large excess of strong alcohol, where it is allowed to remain for several weeks; by this means the proteids are thoroughly coagulated; the alcohol is then filtered off, and the pieces are dried lightly with filtering-paper, and are then put into concentrated glycerine. The glycerine extract thus obtained is exceedingly active as an amylolytic agent, in many cases with salivary glands, and nearly always so with pancreas. Tested chemically, an extract obtained in this way should give but very slight proteid reactions. Brücke, to obtain the extract already alluded to, exposed the minced mucous membrane of the stomach to a temperature of 95° F. with water containing 5 per cent. phosphoric acid. The extract thus obtained he precipitated with lime-water, and dissolved the precipitate of calcium phosphate in a minimum of dilute hydrogen chloride. He again reprecipitated with lime-water, and again dissolved with dilute hydrogen chloride. The liquid was then shaken up with a solution of cholesterin dissolved in four parts of alcohol to one of ether. The cholesterin which separated and rose to the top was filtered off, was washed with water acidulated with acetic acid, and then with distilled water alone. It carried the pepsin. The moist cholesterin was dissolved in pure ether. The ether was removed, and there remained a watery but very actively peptic solution. From this it is seen that, with some exceptions to be mentioned presently, these diffuse ferments of the animal body are insoluble in ether and alcohol, but are soluble in water, and particularly so in glycerine. The following unorganized ferments have been distinguished in the animal body:—

* Dumas, "Comptes Rendus," vol. lxxv. p. 295.

† Moleschott's "Untersuch.," vi. 1869, p. 479.

I.—Amylolytic or Diastatic ferments—*i. e.*, the ferments which convert starch or amyloids into grape-sugar or dextrose. These are :—

a. Ptyalin, found in the salivary glands, and by Cohnheim in the urine. In man the saliva of both the submaxillary and parotid glands contains this ferment.

b. Amylopsin,* found in the pancreas, and separated by Cohnheim and Danilewski.† This ferment is much more rapid and energetic in its action than ptyalin.

c. A ferment‡ found in the *liver*, which converts glycogen into sugar.

d. A ferment found in the *bile*, which is capable of converting starch into sugar; its action, however, is but of minor importance.

e. A ferment found in the *blood*, which is probably the same as that found in the liver, since it has the same properties.

f. A ferment found in the *gastric and intestinal mucous membrane*§ of the dog and horse.

g. In most animals an amylolytic ferment can be obtained from almost any part of the body.

II.—Proteolytic ferments are those which have a distinctive action upon proteid compounds. They are :—

a. Pepsin, found in the peptic glands of the mucous membrane of the stomach, and by Brücke in the blood, muscles, and urine; like the amylolytic ferment, pepsin is very widely distributed in the body. Its action is one of solution, and it is active only in an acid medium.

b. Trypsin or *Myopsin*‖ is the proteolytic ferment of the pancreas. It converts albumins into peptones, and ultimately into leucin and tyrosin. It is active only in an alkaline medium, and its action is one of corrosion. It appears to be produced in the pancreas under somewhat different circumstances from the amylopsin already mentioned. Trypsin has also been found in the urine.¶ It is active, according to Salkowski, after it has been heated to 160° F.

c. Two ferments found in the saliva—one by Hüfner, which is active in alkaline media only; and a second by Munk** in the mixed human saliva, which is active only in acid solutions.

III.—Inversive ferments which are capable of transforming cane-sugar into dextrose and levulose :—

a. Such a ferment was found by Cl. Bernard in the Succus entericus; it may also possibly act as a proteolytic ferment.

b. A ferment found in the mucin of the stomach. This ferment is analogous to, but quite distinct from, ptyalin.††

c. A ferment obtained by Bertholet from the tissue of the testis; it converts glycerine and mannite into glucose.

IV.—The ferment which is probably contained in the white blood corpuscles, which brings about the union of fibrinogen with fibrinoplastin to form fibrin in blood coagulation (q.v.).

V.—*Ferments with an action on fat* :—

* Th. Defresne, "Séance Acad. des Sci.," June 10, 1878.

† Virchow's "Archiv," xxv. p. 279.

‡ Von Wittich, "Archiv f. Physiol," vii. p. 28.

§ "Centralblatt f. Med. Wissensch.," Aug. 11, 1877.

‖ Virchow's "Archiv," lxx. p. 158.

¶ Brunton and Power "On the Albuminous Substances contained in the Urine," St. Bartholomew's Hospital Reports, 1877, p. 310.

** "Deutsche Med. Wochenschrift," 1876, No. 48; and "Centralblatt f. Med. Wiss.," 1877, p. 582.

†† Foster, "Physiology," 2nd ed. p. 189.

Steapsin,* a special ferment present in the pancreas which has the power of breaking up fats into glycerine and the corresponding fatty acids.

The emulsifying power which the pancreatic juice exerts upon fats is not due to any special ferment, but is dependent, in all probability, upon the presence of alkali albumin.

A special ferment in the spleen, which is said to split up fats into glycerine and the corresponding fatty acids; the existence of this ferment is somewhat hypothetical.

VI.—A special ferment contained in the gastric juice which has the power of curdling milk, probably by the conversion of the lactose or milk-sugar into lactic acid; when this happens the casein is precipitated.†

In describing the method of isolating unorganized ferments, it was stated that there were certain exceptions in which a ferment could not be obtained by the method there indicated. This is the case with trypsin, the proteolytic ferment of the pancreas; for if the gland be removed from an animal immediately after death, the glycerine extract has no power of digesting fibrin unless it be treated with a dilute acid, such as hydrochloric or acetic. It is thus necessary under ordinary circumstances to keep the pancreas for some hours after death before proceeding to make an extract of it. In the same way, a piece of boiled liver, in which no sugar could be detected, has been found to contain sugar after the lapse of twenty-four hours. Again, certain extracts of pancreas, such as those made from a fasting animal, are found to be inactive towards proteids, whilst extracts of salivary glands are inactive in relation to starch. In each case the addition of dilute hydrogen chloride causes them to become active; so also an inert solution of pepsin becomes active on the addition of hydrochloric acid. Now these results all point to the fact that the ferment, as such, is not present in the gland in an active condition, but that it only becomes capable of exerting its peculiar function after it has undergone some change; in other words, the ferment is produced directly from some other substance. It is this substance to which the name Zymogen (the mother of ferment) is applied as a general term. Assuming that Zymogen really exists, there arises a question as to the relation in which it stands to the various ferments of the body, whether as their common origin, or whether other intermediate substances intervene. In the latter case, which is by some assumed to be true, the intermediate substances have received special names in the case of the stomach and pancreas; thus, the substance producing pepsin is termed Pepsinogen, whilst that which gives rise to trypsin is similarly Trypsinogen. As yet but little is known of these bodies, it being supposed, on theoretical grounds, that Trypsinogen is soluble in glycerine, whilst Pepsinogen is insoluble in the same medium. Neither body has yet been isolated.

It is stated,‡ apparently however upon insufficient evidence, that trypsin ceases to be present, or at any rate ceases to be active, in the pancreatic secretion after extirpation of the spleen. There is as yet no answer to the question whether Zymogen is the common product from which trypsin, pepsin, ptyalin, &c., take their origin; it is known, however, that these, the resultant ferments, are distinct, not only from their mode of action, but also from the fact that trypsin, which probably contains nitrogen in considerable quantity and is proteid in nature, is capable of being digested by pepsin. Of the formation of Zymogen, which appears to be a long and toilsome process, and of its conversion into ferment, if such occur, we know but little.

* Th. Dufresne, "Acad. des Sci.," June 10, 1877.

† Foster, "Physiology," 2nd ed. p. 195.

‡ Schiff, "Schweiz. Zeitsch. f. Heilkund," i. 1862, p. 209.

Derivatives of Albumin.

56. Collagen, Gelatin, or Glutin.—Collagen is pure connective tissue. Gelatin and glutin do not pre-exist in it, but may be obtained by boiling connective tissue, articular fibro-cartilage, or bone with water, especially if this be slightly acidified. The solution gelatinizes, even when gelatin is only present in the proportion of 1 per cent.; many salts, however—as common salt, nitre, and ammonium chloride, as well as dilute acids—prevent solutions of gelatin from setting. Pure gelatin is a colloid and is colourless, transparent, and destitute of taste and smell. Its solutions are precipitated by alcohol and ether, but not by acids, with the exception of tannic acid, which constitutes its most delicate test. It is also precipitated by chlorine water and corrosive sublimate, but not by other salts of mercury, nor by those of silver, copper, lead, or alum, nor by potassium, ferro- or ferricyanide. Solutions of gelatin do not dialyze. They possess a levo-rotatory power which at 25° C. (77° F.) = −130°, and at 40° C. (104° F.) = −123°. Gelatin is soluble in a large quantity of glycerine. The per-centage formula of gelatin is given somewhat differently. Scherer, experimenting with gelatin from tendon, obtained C 50·9, H 7·2, N 18·3, O 23. When exposed to the action of concentrated acids, alkalies, and oxidizing agents, gelatin behaves like the albuminous compounds generally, yielding amongst other products leucin and glycin.

Elastin is the basis of elastic tissue, and may be obtained in a pure state from the ligamentum nuchæ by boiling it successively with alcohol, ether, water, concentrated acetic acid, dilute solution of potash, and hydrochloric acid. When the residue is thoroughly washed it forms a yellowish fibrous mass, still possessing great elasticity, which dissolves in concentrated alkalies and in sulphuric acid, which last decomposes it, giving rise to leucin. With nitric acid it gives the xanthoproteic reaction. Heated on platinum it burns away without leaving any residue. It contains no sulphur. The per-centage formula is C 55·5, H 7·4, N 16·7, O 20·4 (Hofmann).

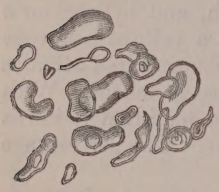
Chondrin is obtained by heating permanent cartilage freed from periosteum, or the cornea of the eye, with water in a Papin's digester at a temperature of 120° C. (248° F.) for three hours, filtering whilst hot, precipitating with acetic acid, washing and removing all traces of fat with alcohol and ether. It forms a hard transparent yellowish mass, insoluble in ether and alcohol, and separating from its hot aqueous solutions, which have a levo-rotatory power, in a gelatinous form. It appears to be a modification of gelatin, from which it differs in being precipitated by acetic acid: the precipitate being soluble in potassium, ferro- and ferricyanide, which distinguishes it from albumin. It is also precipitated by dilute mineral acids and by the salts of alum, iron, lead, silver, and copper, whilst its solutions are only rendered slightly turbid by tannic acid. When boiled with sulphuric acid it yields glycin, but no leucin. It is not as yet accurately ascertained whether gelatin and chondrin pre-exist in the tissues from which they are obtained, or are produced by the act of boiling, for, on the one hand they cannot be obtained by maceration in cold water, whilst, on the other, the action of tannic acid on the tissues seems to be of the same nature as on the solution, and when exerted upon the connective tissues of the skin converts it into leather. Its per-centage composition is C 50, H 6·6, N 14·4, O 20·6. When subjected to the action of hydrochloric acid, or of gastric digestion, chondrin yields a kind of sugar named *Chondroglycose*.

Keratin constitutes the basis of the various horny tissues, as epithelium, epidermis, nails, hoofs, claws, horn, wool, hair, and feathers. It can be obtained from the brain by peptic digestion. It is characterized by swelling

and becoming soft in boiling water, though it neither dissolves in this fluid unless the temperature is much raised by pressure, nor in ether or alcohol. With the exception of hair the tissues in which it is contained are soluble in acetic acid and in alkalies. It is coloured yellow by nitric acid, and under the action of sulphuric acid developes much leucin and tyrosin. The horny tissues in their early state are all composed of soft cells, which subsequently become modified in form, and much firmer in consistence. They contain C H N O and S in proportions that, whilst closely similar to those of the albuminous compounds from which they are derived, have not yet been accurately determined.

Mucin.—A substance possessing in a high degree the power of absorbing water, and swelling up to a gelatinous and sticky mass of semi-fluid consistence which is incapable of dialyzing. No precipitate or coagulation occurs in mucin at a boiling heat, nor is any produced by acetic acid, the mineral acids, or potassium ferrocyanide. It occurs in the body in the mucous fluids, and may be obtained by boiling water from the fœtal connective tissue. It is contained in the fluid of Ranula. Its per-centage composition is given as C 49·5, N 9·6, H 6·7, O 34·2, and it therefore differs from albumin in being free from sulphur, and in containing a smaller amount of carbon and nitrogen. The substance formerly named *Pyin*, and obtained from pus, is probably only a mixture of various albuminous compounds.*

Fig. 48.



Myelin.

Cerebrin.—This substance, the exact composition of which is not known, is obtained from pus-cells and from nerve-tissue by a complicated process. It forms a white light powder destitute of taste and smell, and composed of roundish granules. At 80° C. it reddens, then swells up, and at higher temperatures melts and burns. It is soluble in boiling ether and alcohol. Moist cerebrin, especially if not freed from admixture of lecithin and cholesterin, exhibits the so-called Myelin forms—which are double-edged drops strongly refracting light, and which extend and contract themselves, and perform peristaltic movements.

Protagon, formerly regarded as a constituent of nerve-tissue, appears to be a mixture of cerebrin and lecithin.

Nuclein, $C_{29}H_{49}N_9P_3O_{22}$.—This substance was first obtained by Miescher from the nuclei of pus corpuscles,† and afterwards from the yolk of egg, the spermatozoa of salmon and other fish, and of the bull. Hoppe-Seyler extracted it from yeast, from the cells of a papillomatous tumour, and the bran of wheat; and Plosz separated it from the nuclei of the red corpuscles of birds; traces of it have been found in the liver and in the brain. It may best be obtained by digesting pus corpuscles with warm alcohol, removing the albuminous compounds by peptic digestion and purification with alcohol ether and solution of soda, by which last part is dissolved. On the addition of hydrochloric acid this part precipitates and is washed with alcohol. The remainder is *soluble nuclein*. It dissolves in alkaline fluids, forming pale-yellow solutions, and is precipitated by hydrochloric and acetic acids. It is insoluble in water and in solutions of common salt. In its reactions it resembles Lardacein. That part which does not readily dissolve in solution of soda is *insoluble nuclein*, so called because it dissolves very slowly in caustic alkalies and in strong hydrochloric acid, and not at all in glacial acetic acid, even when heated for hours at 140° C.

Nuclein‡ is not attacked by any of the digestive ferments, and may be

* Hofmann's "Lehrb. d. Zoochemie," p. 8, 1878.

† Hoppe-Seyler's "Med. Chem. Untersuch.," Heft iv. pp. 441, 502.

‡ A. Bókay, "Zeits. f. Phys. Chemie," Band i. p. 157.

egarded in all probability as a constant constituent of the fæces, since it is ontained in the greater number of alimentary substances.

If the recent researches of Morochowetz be correct,* nuclein, mucin, and myloid substance are identical. They all contain phosphorus, though the proportion slightly differs—mucin, for example, containing 2·45 per cent., and myloid substance 3 per cent. Their chemical reactions appear to be identical.†

Carnin, $C_7H_8N_4O_3 + H_2O$.—A base that has been obtained by a complicated process from American meat extract.‡ It forms a white friable mass composed of bitter crystals, easily soluble in boiling water, insoluble in alcohol and ether. Its solution is neutral. When treated with bromine or chlorine, or with hot nitric acid, it forms a salt of Sarkin. It contains the elements of Sarkin and of acetic acid ($C_5H_5N_4O$ and $C_2H_4O_2$), and only differs from theobromine in having one more atom of oxygen. Its physiological value and action are unknown.

Lardacein.—A peculiar form of degeneration, formerly known and described under the name of "amyloid" or "waxy" degeneration, takes place in certain tissues and glands. It appears to be due to a metamorphosis of albumin and the formation of a nitrogenous compound, termed Lardacein. This is best obtained by mincing the affected liver or spleen; removing the vessels as far as possible; extracting with cold water; boiling the residue with water to remove connective tissue in the form of gelatin, and with alcohol and ether to remove cholesterin and fat, and finally with alcohol containing common salt. The mass is subjected to the action of a powerful digestive fluid at 40° C. as long as the filtrate reacts to xanthoproteic and peptone tests. It is then boiled once more with solution of common salt in alcohol, and the dry mass is triturated with water to separate elastic fibres. It is amorphous, friable, insoluble in water, alcohol, ether, diluted hydrochloric or acetic acid. It is not capable of conversion into peptone, and is not liable to putrefaction. It is soluble in moderately concentrated ammonia and in strong hydrochloric acid. Iodine stains it reddish-brown or violet, or even blue. Methylanilin stains it red. Its per-centage composition is C 53·60, H 7, N 15·53, O 22·53, S 1·30.

Aleuron§ is an azotized substance of complex constitution, found in some parts of animals, and even more widely distributed in the vegetable kingdom than starch; it was discovered in 1855 by Hartig. It is found in every part of plants, as in the wood, bark, roots, and seeds. In oleaginous seed it forms the largest and most important part of the perisperm. In order to obtain aleuron, the parts containing it are washed in oil as starch is washed in water; on standing it is deposited from the oil in the form of a fine powder, which is purified by the action of alcohol and ether. Under the microscope it appears in the form of small ovoid or spheroidal grains, varying from $0^{mm}{\cdot}00125$ to $0^{mm}{\cdot}0375$. M. Hartig has applied the term "solitaires" to the large grains found amongst those that occupy a cell, as in Bertholletia and Corylus; and "grains comblants" to those which are so large as to fill a cell by themselves, as in Myrtus and Juglans. Aleuron grains are usually colourless, but may be green (Pistacia), indigo-blue (Matthiola seeds), rose-red (Hibiscus), yellow

* "Petersburger Med. Wochens," No. 10, 1878.

† According to Hake and Kingzett ("Quart. Journ. of Science," Jan., 1877, and "Animal Chemistry," 1878, pp. 278 and 359), the presence of phosphorus in the various published papers on the composition of Nuclein clearly shows the impurity of the preparation, and its contamination with Lecithin. Worm Müller (Pflüger's "Archiv," Band viii. p. 190) also regards it as an impure albuminous substance. (See "Animal Chemistry.")

‡ By Weidel, "Ann. Chem. Pharm.," Band clviii. p. 353.

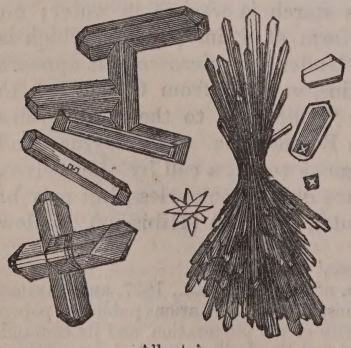
§ ἄλευρον, starch. F. aleuron., G. Klebermehl.

(Lupinus), or brown (Arachis). The grains appear to be vesicles, foveolated on the exterior; and the contents consist of the proper aleuronic matter and one or more "albines," "globides," "crystalloides," or "noyaux blancs." The albine is colourless and embedded in a vacuole or depression of the body of the grain. Many aleuron grains under the influence of water, or of iodine and water, assume a crystalline form, as rhombohedral in Sparganium; octohedra in Viola; hexahedral in Magnolia; cubic in Camarina; tetrahedral in Juniperus. All forms of aleuron grains present two characteristic reactions. A solution of iodine in water, alcohol, or glycerine stains them of a yellowish brown colour, while a solution of mercury nitrate with a drop or two of nitric acid renders them brick-red. They are soluble in water, acids, diluted alkalies and, though more slowly in glycerine, they are insoluble in alcohol, ether, and in fixed and volatile oils. Their chemical composition is not accurately known, but they contain nitrogen and are probably to be classed with the albuminous compounds. M. Hartig considers that they contain fibrin, albumin, gliadin, and casein, with which are mingled gum, sugar, and mineral salts. Like starch, from which it appears to be in some instances developed, it is of the nature of a store of reserve-nutriment. Aleuron crystals are also found in the vitellus of the ovum of vertebrated animals, forming the "yolk laminæ" of some authors. Hoppe-Seyler regards them as one of the products of the metabolic processes taking place in the protoplasmic matter of cells, but not as a true constituent of it.

Lutein.—This term has been applied by Dr. Thudichum* to a yellow substance crystallizable in rhombic plates, which can be obtained from various parts of animals and plants. It is normally present in the vitellus of the egg, in the corpora lutea of the ovary, and in the serum of blood, the cells of fat, and under pathological conditions in ovarian tumours and in serous effusions. It is also contained in the seeds, roots, leaves, and stamens of many plants. It is easily soluble in alcohol, ether, and chloroform, but is insoluble in water. Its spectrum presents three absorption bands in the blue, indigo, and violet portions of the spectrum. It crystallizes and exhibits strong attraction both for fatty and for albuminous substances. The substance termed Hæmatoidin by Holer and Städeler is Lutein; but the Hæmatoidin of Valentiner, Robin, Ruhe, and Mercier is Bilirubin or Cholophæin.

Allantoin, $C_4H_6N_4O_3$.—As its name implies, this substance is found in the allantoic fluid of the cow, but it also appears in the acid urine of fœtal and sucking animals—that is, during the period of life when the herbivora are subsisting on animal food. It has also been found in human urine after the free use of tannic acid. It crystallizes in the form of transparent rhombohedral prisms, soluble with difficulty in cold, but more easily in hot water and in boiling alcohol. It is insoluble in ether. It is closely allied to uric acid and to urea—in fact, under the influence of yeast it breaks up into urea and salts of ammonia,—and is consequently one of the terminal products of the disintegration of albumin. It is not precipitated by corrosive sublimate nor by the salts of lead. It has been found in the urine of dogs suffering from diseases of the lungs, apparently in consequence of the

Fig. 49.



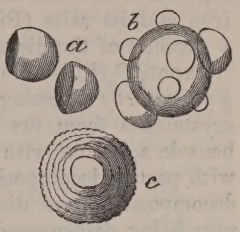
Allantoin.

* "Centralblatt," 1869, p. 1.

eficient supply of oxygen impeding the formation of the uric acid ordinarily resent.

Leucin, $C_6H_{13}NO_2$, or Amido-caproic acid, $C_6H_{11}(N_2H)O_2$, appears in the form of iridescent scales which are made up of fine microscopic needles, but often also in the form of spheroid or hemispheroidal masses, or of an aggregate of one large spheroid with several smaller ones adherent to it. The spheroids either present a concentric lamination or are destitute of this and resemble fat cells. It is destitute of taste and smell, is soluble in 27 parts of cold water, and in 625 parts of cold alcohol, sp. gr. 0·82. Its aqueous solution is neutral. It melts at 170° C. It unites both with acids and with bases. It was first discovered in putrid cheese, and is largely present in the pancreas and pancreatic juice, and is also found in the salivary glands and saliva, in the spleen, kidneys, and supra-renal bodies; in the thymus, thryoid and lymphatic glands, in the fluids of the lungs, and in pus, and occasionally in the urine, especially in cases of acute atrophy of the liver. It is either absent or only traces of it can be found in the healthy liver, brain, and muscles. It is in all probability a product of the retrogressive metamorphosis of gland tissue. It has been artificially obtained by Kühne from the action of the pancreatic ferment on albumen. Frerichs and Städeler have shown it to be probable that it undergoes decomposition in the alimentary canal, into ammonia, and the volatile fatty acids.

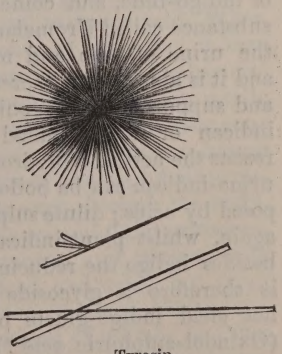
Fig. 50.



Leucin.

Tyrosin, $C_9H_{11}NO_3$.—This substance is obtained by boiling for sixteen hours one part of horn shavings with twelve times its weight of a 20 per-cent. solution of sulphuric acid, adding water. It is likewise an amido-acid and forms delicate white silky needles, which have no taste or smell, are soluble in 1900 parts of cold water and in 150 of hot, as well as in acids and alkalies. It is insoluble in alcohol and ether. When its solution is warmed with mercury nitrate the solution first assumes a beautiful red colour, and then quickly throws down a dark-brown red precipitate (Hoffmann's test). It may be obtained by boiling horn shavings or any form of albumen with strong sulphuric acid. The fluid is diluted and neutralized with milk of lime, and filtered from the gypsum. It is then evaporated, acidified with sulphuric acid, and filtered. White lead is then rubbed up with the filtrate, and a soluble tyrosin-lead is formed. The lead is precipitated with hydrogen sulphide, and the remaining fluid evaporated till the tyrosin crystallizes out. About one per cent. of tyrosin can be obtained from Ovalbumin and muscle fibrin, and about two per cent. from blood fibrin. It is contained in decaying cheese, from which it may be abstracted by water, and purified in the way above given. Tyrosin is said to be found in the spleen and pancreas, and in acute atrophy of the liver in that gland, in the brain, and in the urine; but it is probable, from Radziejewsky's researches,* that it never occurs in any organ in a normal condition, with the single exception

Fig. 51.



Tyrosin.

* Virchow's "Archiv," 1866, May.

of the contents of the small intestines, where it results from the decomposition of albuminous compounds under the influence of the pancreatic juice. Heated with concentrated sulphuric acid it forms Tyrosin-sulphuric acid together with other acids. The former gives a beautiful violet colour, with iron and its salts (Piria's test). Tyrosin, like Leucin, is to be regarded as a product of the disintegration of the albuminous compounds.

INDOL, C_8H_7N.—This substance is produced in a quantity amounting to $\frac{1}{2}$ per cent. by digesting serum-albumin or egg-albumin with pancreatic juice. It crystallizes from hot water in large shining colourless laminæ, resembling benzoic acid, but with a peculiarly nauseous smell. It melts at 52° C.; boils with partial decomposition at about 245° C.; volatilizes in a vacuum without decomposition, and distils easily with vapour of water. It is a weak base, its salts being decomposed by boiling with water. Its vapour colours a deal shaving, moistened with hydrochloric acid, deep cherry-red. Indol fused with potash is converted into anilin. Ozone passed through an aqueous solution of indol forms a small quantity of indigo-blue. It is met with in the intestinal canal as one of the products of digestion, but its precise mode of origin is unknown. Jaffe* found that on obstructing the passage of the bowels there was a remarkable increase in the amount of indigo-forming substance in the intestine, a result that was also obtained when indol was directly introduced into the intestine, the quantity of indigo being in direct proportion to the quantity of indol introduced. It would appear that indigo-forming substance is constantly present in the urine of animals fed exclusively on flesh,† and that, speaking generally, when an excess of albuminous food is consumed a similar substance appears; though when the supply of proteids is moderate and the processes of digestion and absorption are rapidly and energetically performed none is produced.

INDICAN (*Uroxanthin*), $C_{26}H_{31}NO_{17}$.—The indican, derived from Woad, the *Isatis tinctoria*, is a clear brown, intensely bitter and nauseous syrup, with neutral reaction, soluble in alcohol and ether. Its solutions are precipitated by lead acetate and ammonia. When treated with acids it breaks up into Indigo-blue and Indigo-glucin, whilst indigo-red (Heller's *Urrhodin*, Schunk's *Indigorubin*), leucin, and the fatty acids are also formed in small quantity. The same or similar changes are effected in it by ferments, especially by that associated with the putrefaction of urine. The addition of calcium chloride or a trace of chlorine gas to acid solutions of Indican causes immediate precipitation of indigo-blue, and coincidentally a substance which closely agrees with the substance called Uromelanin, $C_{36}H_{43}N_7O_{10}$. Indican is a normal constituent of the urine of man and mammals, the quantity being greatest on flesh food, and it is abnormally increased in cancer of the liver, cholera, Addison's disease, and suppurative peritonitis. Urine-indican is not identical with plant-indican or that obtained from the *Isatis tinctoria*, for whilst plant-indican resists the action of hydrochloric acid and is quickly decomposed by alkalies, urine-indican can be boiled with alkalies without change and is rapidly decomposed by acids; dilute sulphuric acid, however, having little action on it. And, again, whilst plant-indican, as just stated, on the addition of acids yields besides indigo the reducing but not fermentable substance indigo-glucin, and is therefore a glycoside; urine-indican under the same conditions does not yield indigo-glucin but sulphuric acid, and is an ether of this acid (Oxindol-sulphuric acid?).

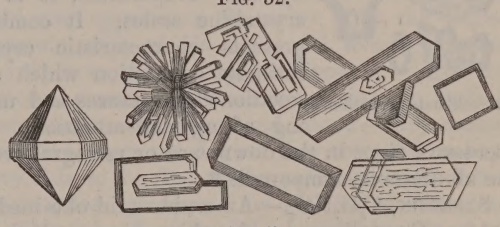
INDIGO, $C_{16}H_8N_2O_2$.—This may be obtained from the urine of the horse by evaporating to a syrup, adding an equal volume of strong hydrochloric acid,

* Virchow's "Archiv," 370, p. 1, 1877. † Hoppe-Seyler, "Physiol. Chem.," p. 333, 1878.

to which a little chlorine gas is added, so that a blue colour appears, and setting aside for twelve hours the precipitate is collected on an asbestos filter, washed with boiling water, and then with alcohol, and finally dried. It is a dark-blue powder, consisting of needles, or oblique rhombic laminæ. It is insoluble in water, alcohol, ether, alkalies, and dilute acids, but soluble in boiling chloroform, amylic alcohol, and melted paraffin. The solution in amylic alcohol exhibits a dark absorption stria between *d* and D, and the violet end of the spectrum is dark from G onwards. It sublimes at 300° C. in violet vapours. It forms two sulphacids with boiling sulphuric acid, purpursulphuric acid, and sulphindigotic acid. With boiling chromic acid the blue colour vanishes, and on cooling *Isatin*, $C_{16}H_{10}N_2O_4$, is deposited. Isatin on exposure to nascent hydrogen (zinc and hydrochloric acid) forms *Isatyd*, $C_{16}H_{12}N_2O_4$. Watery solution of isatinate of sodium treated with sodium amalgam yields on evaporation crystals of Dioxindol-sodium, from which the sodium may be removed by hydrochloric acid, yielding yellowish rhombic prisms of *Dioxindol* (hydrindin acid), $C_{16}H_{14}N_2O_4$. This exposed to nascent hydrogen is reduced to *Oxindol*, $C_{16}H_{14}N_2O_2$, a colourless substance, crystallizing in needles that are soluble in boiling water and alcohol, which when exposed to heated zinc-dust yields *Indol*, $C_{10}H_{14}N_2$, so that isatin, isatyd, dioxindol, oxindol, and indol—which last is one of the final stages of the decomposition of albuminous compounds—stand in near relation to each other.

Kreatin, or Methylglycocyamin, $C_4H_9N_3O_2$.—This substance is a constant constituent of muscular tissue, both of the striped and smooth variety, in the proportion of from 2 to 4 parts in 1000; and is found in the blood, brain, and amniotic fluid, but not in gland-tissue. It crystallizes with H_2O in oblique rhombic prisms, which are soluble in hot water, but are deposited again on cooling. It dissolves with difficulty in alcohol, and is insoluble in ether. It is prepared by exact precipitation of the phosphates in the juice of meat with acetate of lead; separation of the lead by means of sulphuretted hydrogen and careful evaporation. It is a weak base. On boiling it with baryta water it is converted into sarkosin—a substance closely related to the glycin of the bile—and urea, which immediately splits up into ammonia and carbonic acid. When heated with acids, or even after long exposure to the action of hot water, it loses two atoms of water and becomes converted into kreatinin. Under other circumstances, instead of producing sarkosin and urea, it may decompose into oxalic acid and a substance termed methyl-guanidin (uramin) which stands in close connection with guanin, xanthin, hypoxanthin, and uric acid; all of which relations are full of interest, in reference to the successive stages or planes of disintegration suffered by the albuminous compounds in their passage through the body, since nearly all of them are found in one or other of the several fluids or tissues.

Fig. 52.



Kreatin.

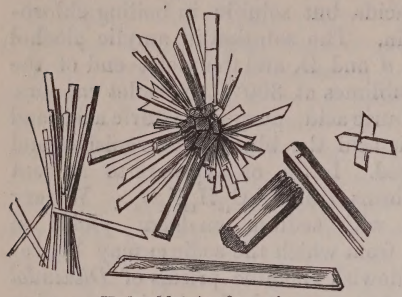
Kreatinin, $C_4H_7N_3O$, is usually associated with kreatin, and consequently occurs in muscular and nervous tissue, and in the blood and urine, but is not found in the glandular textures. Nawrocki,* however, believes his experiments prove satisfactorily that kreatinin is not a constituent of muscle, and that no conversion of kreatin into kreatinin occurs during exercise. As just shown, it may be obtained from the action of acids on kreatin. It is a powerful base,

* Fresenius, "Zeits. f. Analyt. Chemie," Band iv. 2.

and crystallizes in oblique rhombic prisms, which are soluble in water and in boiling alcohol.

GUANIN, $C_5H_5N_5O$.—An amorphous, yellowish-white substance, nearly insoluble in alcohol, ether, and water; easy soluble in acids and alkalies. By oxidation with potassium permanganate, guanin is converted into urea, oxalic acid, and oxyguanin. It constitutes the greater part of the excrements of spiders, but has also been found in the pancreas and liver, in muscle extract, and, as its name imports, in guano. It forms crystalline combinations with various acids, one of which is represented in the adjoining woodcut, and also with lime and soda.

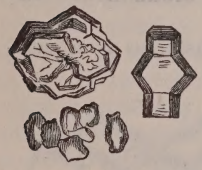
FIG. 53.



Hydrochlorate of guanin.

XANTHIN, $C_5H_4N_4O_2$.—This substance, which was first found in the form of oxide of xanthin in certain rare urinary calculi, is amorphous, and presents, both in its chemical constitution and in the places where it is found, the closest analogy to hypoxanthin. It is soluble in 1400 parts of boiling and 14,500 parts of cold water. It is soluble in ammonia, from which solution, by slow evaporation, it is again deposited in confused crystalline scales. It combines with acids, and then presents characteristic crystalline forms. The very intimate connection which exists between the three last-mentioned substances and uric acid, $C_5H_4N_4O_3$, is deserving of especial attention. They all clearly constitute successive steps in the downward or retrogressive process of metamorphosis of the albuminous compounds.*

FIG. 54.

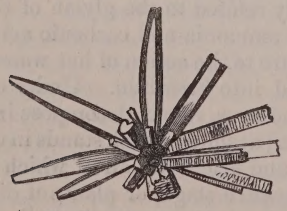


Hydrochlorate of xanthin.

SARKOSIN, $C_3H_7NO_2$.—An amido-acid obtained by boiling kreatin in baryta water. Crystallizes in rhombic prisms. It has not been certainly demonstrated to be a constituent of the body.

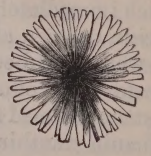
HYPOXANTHIN (*Sarkin*), $C_5H_4N_4O$, appears in the form of colourless, microscopic, crystalline granules, of no recognizable shape, which are soluble

FIG. 55.



Nitrate of hypoxanthin.

FIG. 56.



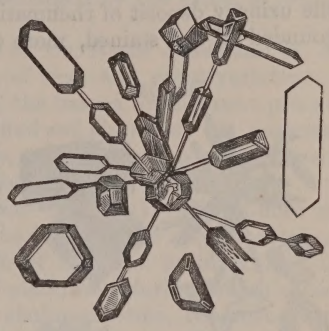
Hydrochlorate of hypoxanthin.

in 300 parts of cold and 76 of hot water, and readily dissolve in acids and alkalies. By nitric acid it is converted into xanthin. It does not appear to be a constituent of the blood in health, though it rapidly appears after death;† but it has been found in the blood and urine of leukæmic patients,‡ in muscle extract, in the liver, spleen, thymus, thyroid, kidney, and brain, and in the medulla of bones. It unites with acids to form salts, which form

* See G. Salomon, "Zeit. f. Chemie," Band ii. 1878, p. 95. † Ibid., Band ii. p. 84.
‡ Salkowski, "Archiv d. Heilkunde," Band xi. p. 1.

well-defined crystals (Figs. 55, 56). The amount of sarkin in muscle varies from 0·016 to 0·028 per cent.

Hippuric Acid, $C_9H_9NO_3$, is a glycocol in the amide group of which an atom of hydrogen is replaced by the radical benzoyl, C_6H_5CO. It is one of the constituents of human urine, though, like the last-named acid, it exists only in small quantity. It is always more abundant in the urine of the herbivorous than in that of carnivorous animals. It may be obtained from the urine of the cow or horse by simple addition of hydrochloric acid, when it crystallizes out; by re-solution and filtration through animal charcoal, it appears in the form of beautiful, transparent, colourless, four-sided prisms, which belong to the rhombic system. They are soluble with difficulty in cold water and in ether, but more easily in hot water and in alcohol. When benzoic acid is ingested, it is eliminated from the body as hippuric acid—a change that probably takes place, in part at the kidney,* but chiefly at the liver, since benzoic forms hippuric acid by taking up glycin and giving off ten equivalents of water, and it is remarkable that all the herbivora secrete bile which is rich in glycin. Hippuric acid also appears in the urine after the ingestion of bitter-almond oil, cinnamic acid, chinic acid, and toluol into the stomach. Meissner and Shephard† have shown that the hippuric acid of the herbivora is directly dependent on the nature of the aliment, since on feeding them with non-albuminous compounds—fat, sugar, and starch—they ceased to pass this acid in the urine, whilst it reappeared when they were fed on hay, straw, or clover. They believe this to be due to the presence in the latter of a body belonging to the benzole atomic group, and by a process of exclusion, that it was the thickened and infiltrated cell-walls of the epidermis cells which furnished the primary substance that by conversion yielded the acid. The most important derivatives of hippuric acid are benzoic acid and glycocol.



Hippuric acid.

Benzoic Acid, $C_7H_6O_2$.—An acid volatilizing at 240° C., crystallizing in needles or scales, soluble with difficulty in cold water, but more readily in hot water, ether, and alcohol; destitute of smell, and tastes sharp; its vapour excites a peculiar tickling in the throat; taken by the stomach in mammals it becomes converted in its passage through the system into hippuric acid, in which state it is eliminated by the kidneys, but this change does not occur in birds. It does not appear to be found in the system, but when found, as in putrefying urine, smegma præputii, and in the sweat, it results from the decomposition of hippuric acid.

Glycocol, $C_2H_5NO_2$.—A product of the disintegration of hippuric acid, obtained by boiling it with strong hydrochloric acid. It is a colourless, hard, stable body, crystallizing in oblique rhombic prisms. It tastes sweet, is insoluble in alcohol and ether, but dissolves in 4 parts of water, and melts and

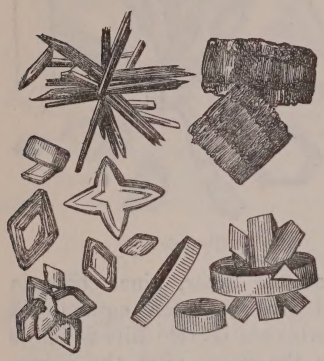
* Meissner and Shephard's "Die Hippursäure," 1866. Bunge and Schmiedeberg, "Archiv f. Exper. Pathol.," vi. 1876, p. 233. In Birds benzoic acid is eliminated, according to Jaffe ("Ber. d. Deutsch. Chem. Gesellsch.," 1877, p. 1925), in the form of a body having the formula $C_{19}H_{20}N_2O_4$, and to which he gives the name of ornithuric acid. See also A. Hofmann "Arch. f. Exper. Pathol.," vii. p. 233; and "Centralblatt," 1878, p. 310.

† "Untersuchungen über d. Entstehen der Hippursäure im thier. Organismus," 1866.

is decomposed at 170° C. It combines with metals, acids, and salts. With nitric acid, glycocol yields glycolic acid, and with ammonium permanganate it yields oxalic and other acids.

Uric Acid, $C_5H_4N_4O_3$.—When perfectly pure, uric acid appears in the form of colourless, microscopic, rhombic crystals, occasionally in six-sided plates, and sometimes in rectangular four-sided prisms; but as they are usually seen in the urinary deposit of rheumatic patients, the angles of the rhombic plates are rounded off and stained, more or less deeply, by the colouring matters of the urine. It is nearly insoluble in water, and completely so in alcohol and ether. It is dissolved by concentrated sulphuric acid, and can be precipitated unaltered on the addition of water. On subjecting it to a high temperature, it decomposes, and yields urea and cyanuric acid; with oxidizing agents, as ozone and peroxide of lead, it gives allantoin, urea, oxalic and carbonic acids. When acted on by nitric acid, and evaporated to dryness, the residue slightly moistened with ammonia assumes a beautiful purple tint from the formation of murexide. Uric acid is found in the urine, the blood, the juice of flesh, and in glandular structures, in all of which it probably exists in the condition of urate of soda. It proceeds from the decomposition of the albuminous compounds, and contains 33 per cent. of nitrogen. The proportion of N to C is as $1 : 2\frac{1}{2}$.

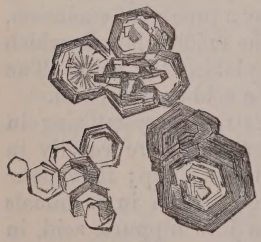
Fig. 58.



Uric acid.

Cystin (*Amido-sulphopyruvic Acid*), $C_3H_7NO_3S$; or, as Gamgee and Dewar* give it, $CH_2(H_2N)CSCO_2H$—A rare constituent of the urine of apparently healthy persons, and of renal and vesical calculi. It is normally present in the kidneys of oxen. It forms transparent, colourless, six-sided plates or tables, insoluble in water and alcohol, but soluble in mineral acids, in oxalic acid, and in caustic and carbonated alkalies. It is, however, precipitated by ammonium carbonate from its acid, and by acetic acid from its alkaline solutions. Like the foregoing substances, it is in all probability a transition stage of the decomposition of albumin or other nearly allied sulphur-holding compound.

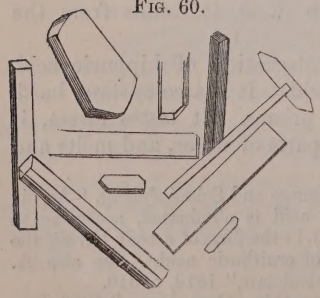
Fig. 59.



Cystin.

Urea, CH_4N_2O—*i.e.*, $(NH_2)_2CO$—crystallizes in white silky, four-sided prisms, which frequently present oblique or dihedral summits. It possesses a bitter cooling taste, like saltpetre, is deliquescent, and very soluble in water and alcohol, but somewhat less so in ether. It has no action on vegetable colours. It is decomposed at 212° F., giving off ammonia. It is not affected by potassium permanganate or ozone, but by nitric acid it is decomposed into water, nitrogen, and carbonic acid. Strong mineral acids, and the hydrates of the alkalies, as well as contact with albuminous compounds

Fig. 60.



Urea.

* "Journal of Anat. and Phys.," vol. v. p. 143.

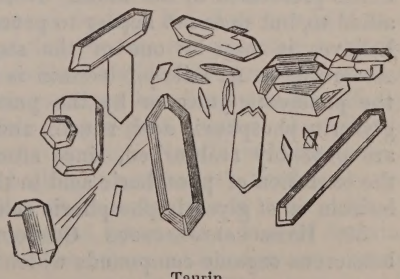
undergoing putrefaction, effect its conversion into ammonium carbonate. It unites with nitric and oxalic acids to form salts. It is isomeric with ammonium cyanate, contains 46 per cent. of nitrogen, and is one of the terminal products of the retrogressive metamorphosis of the albuminous compounds in man. Its extreme solubility, and the facility with which as a "crystalloid" it permeates animal membranes, permit it to be readily discharged by the urine, of which it is the most important organic constituent.

Animal Quinoidin.—From the experiments of Dr. Bence Jones and M. A. Dupré,* it appears there exists in the bodies of man and other vertebrata a substance which can be extracted from any of the tissues by the same process as quinine, when that alkaloid has been ingested and absorbed. It possesses nearly the same chemical properties as quinine, and its solutions give the well-known fluorescence characteristic of that alkaloid.

57. Biliary Compounds.—Cholin (*Bilineurin—Sinkalin*).—Cholin does not seem to exist in a free state in any part of the body, but it may be obtained by breaking up the lecithin contained in yolk of egg, the brain or bile, by means of boiling baryta water, the addition of platinum chloride, which causes a precipitate of a double salt of platinum and cholin chloride, treatment with hydrogen sulphide, and the decomposition of the cholin chloride with moist silver oxide. It is a thick syrup easily soluble in alcohol and water, which turns litmus-paper blue. A dilute watery solution prevents the coagulation of albumen, and dissolves both coagulated albumen and fibrin. In many points it resembles the alkaline bases. Cholin has curious relations to some well-known poisons derived from the Fungi. Thus it appears to be identical with Amanitin, the active principle of the *Amanita muscaria*, and by oxidation with nitric acid it yields Muscarin. On being heated, cholin breaks up into trimethylamin and ethyl-glycol. If the watery solution be treated with iodine water, large transparent prisms are obtained named trimethyliodo-ethyl ammonium-iodide having the formula $C_5H_{13}NI_2$, and which on heating loses the two equivalents of iodine, and is converted into Tri-methyl-vinyl-ammonium-hydroxyd, which is Liebreich's "Neurin." When heated cholin breaks up into glycol and trimethylamin, $N(CH_3)_3$. Now trimethylamin is of frequent occurrence as a result of post-mortem changes, and is probably derived immediately from the cholin, and more remotely from lecithin.

Cholalic Acid or Cholic Acid, $C_{24}H_{40}O_5$, is obtained from glycocholic acid by the action of alkalies. It crystallizes either in four-sided prisms with dihedral summits, in octahedra, or in tetrahedra, which are easily soluble in alcohol, but not readily in water or ether. On boiling with acids, or on being heated to 200° C., it yields Dyslysin ($C_{24}H_{36}O_3$), which is only soluble in ether. Cholic acid has a pure bitter taste, and when treated with nitric acid it yields acetic, valerianic, capronic, oxalic, and cholesterinic acids. One form rotates polarized light 35° to the right, the other 50°.

Fig. 61.



Taurin.

Taurin, $C_2H_7NO_3S$, is found as a constant constituent of the bile in combination with cholic acid. It has also been occasionally discovered in the blood and urine, in the tissue of the kidney, lungs, and of the striated muscles. It forms large tasteless and colourless four- or six-sided prisms, with four-sided

* "Proceedings of the Royal Society," vol. xv. No. 83, p. 73.

pyramids at their extremities. It dissolves in fifteen parts of cold water, and the solution is neutral to test-paper. Taurin is decomposed when subjected to a heat greater than 464° F.

Glycin (*Glycocol, Glycocin, or Gum Sugar*), $C_2H_3(NH_2)O_2$, is chiefly found in combination with cholic acid in the bile, but it also occurs combined with benzoic acid, as hippuric acid, in the blood and urine. It crystallizes in large colourless rhombohedral crystals, which melt at 354° F., are easily soluble in water, but with difficulty in alcohol. The solutions are acid to test-paper, and sweet to the taste. It acts both as a base to acids, and as an acid to alkalies. It originates as the product of the disintegration of gelatin and of albumin, and has been artificially formed.

Glycocholic and Taurocholic Acids, $C_{26}H_{43}NO_6$ and $C_{26}H_{45}NO_7S$.—When to a solution of crystallized ox-bile neutral acetate of lead is added, a precipitate of glycocholic acid in combination with the oxide of lead falls, and when this has been removed by filtration, the addition of the subacetate of lead to the mother liquid causes the precipitation of the taurocholate of the same metal. The amount of glycocholic acid contained in the bile of man and of the carnivora is small, but in that of the ox it is abundant. Both acids rotate the plane of polarized light to the right. Taurocholic acid is easily soluble in water, and tastes very bitter. Glycocholic acid dissolves with difficulty. Glycocholate of soda crystallizes in acicular radiating needles. Taurocholate of soda forms resinous drops. In alcoholic solution it rotates the plane of polarization towards the right 24°.5.* Pettenkofer's test for bile consists in the addition of a little cane sugar, and then of a drop of sulphuric acid to the suspected liquid, when, if either of the biliary acids be present, the fluid ssumes a bright cherry colour, which gradually deepens to purple. Nothing is accurately known respecting the origin of the biliary substances just noticed; but they are probably formed in the liver, and result from the decomposition of albuminous and oleaginous compounds.

Lecithin, $C_{44}H_{90}NPO_9$ or $C_{42}H_{84}NPO_9$, a substance regarded by Diaconow† as distearyl-glycerin-phosphate of cholin, presents the characters of a wax-like body, crystallizing with difficulty in needles from its alcoholic solution below 0° C., easily fusible, hygroscopic, soluble in alcohol, ether, chloroform, carbondisulphide, benzene, hot glacial acetic acid, and the fixed oils; on the application of heat it breaks up into cholin, stearic acid, and glycerin-phosphoric acid. Lecithin is found in all cells undergoing, or capable of undergoing development, as in the yolk of eggs, spermatozoa, white blood corpuscles, rapidly-growing tumours, the seeds and spores of plants, buds in spring, fungi, and yeast-cells; indeed, wherever vigorous metabolism is in process. It exists preformed in the brain. Nothing is known of its origin. It is closely allied to, but does not appear to proceed from, the fats. Hoppe-Seyler, indeed, believes it may be one of the steps towards the formation of the fats. According to A. Bókay,‡ lecithin is decomposed by the oleolytic ferment of the pancreatic juice or by the putrefactive ferment of the intestines into glycerin-phosphoric acid, neurin, and fatty acids. These, in the form of salts, are probably reabsorbed, since after the ingestion of lecithin with the food the excretion of phosphoric acid in the urine is augmented, whilst no trace of lecithin or of glycerin-phosphoric acid is discoverable in the fæces.

58. Hydrocarbonaceous Compounds.—The non-azotized or hydrocarbonaceous organic compounds which are used as food or which enter into the

* Dalton, "Human Physiology," 1876, p. 106.
† "Centralblatt, f. d. Med. Wiss.," 1868, Nos. 1, 7, and 28.
‡ "Zeits. fur Phys. Chemie," Band i. p. 164, 1878.

composition of the body may be divided into two groups, the saccharine and the oleaginous. The principal saccharine substances are starch, milk and grape sugar, inosit, glycogen, and the acids resulting from their fermentation. The chief oleaginous compounds are olein, stearin, palmitin, and cholesterin. Both the oily and the saccharine groups are of great importance in the processes of nutrition and development, and are scarcely ever absent either in the food, the blood, or the tissues. There can be little question that although the saccharine compounds contained in the body are chiefly derived from the farinaceous and saccharine, they partly proceed from the decomposition of the albuminous compounds, the latter change occurring especially in the liver. That a great part of the saccharine and amyloid compounds is derived directly from the food is clearly shown by the following experiment of M. Bernard.* The muscular tissue of a fasting horse was found on careful examination to be perfectly free from amyloid substances; but in the muscles of the same animal, a few hours after a full meal, clear evidence of their presence was obtained. It seems to be well established that compounds presenting a close analogy to sugar may also be obtained by the metamorphosis of oleaginous, as well as of albuminous substances within the body, of which we have examples in their continued formation in the liver, when completely absent in the food, and even during the last stages of inanition, and in their presence and gradual increase in the egg during incubation. The small quantity of sugar naturally present in the blood aids in retaining the carbonate and phosphate of lime in solution, and, according to Hoppe,† assists that metamorphosis by which fat is generated from the albuminous compounds. Most of the saccharine compounds are soluble in water and alcohol, rotate the plane of polarized light to the right, can be obtained in crystals, lose their water of crystallization at a temperature of 212°, at a little higher temperature are converted into a blackish substance termed caramel, and at a red heat are completely decomposed into carbonic oxide, carbonic acid, carburetted hydrogen, acetic acid, acetone, and other products. With oxide of lead and some other bases they play the part of an acid; on fermentation, they either yield alcohol and carbonic acid, or lactic, butyric, and formic acids.

Starch.—This is by far the most important of the hydro-carbonaceous compounds. It exists in the roots, tubers, stems, leaves, fruit, and seeds of plants, both as an amorphous and as a morphological constituent. In the former condition it is comparatively rare, but in the latter it appears in the form of separate granules, presenting, as may be well seen in potato starch, a series of laminæ arranged around an eccentrically situated point. Every starch granule consists of three kinds of substance—of *granulose*, which is coloured blue by iodine; of *erythrogranulose*, which is coloured red by it; and of *cellulose*, which is not coloured by it. If iodine be added to a starch granule, it becomes of a deep blue tint, because the granulose is by far the largest constituent; but if very little iodine be added the granule becomes of a reddish colour, because the erythrogranulose has the strongest affinity for it, and seizes upon it. On boiling with a 2 per-cent. solution of sulphuric acid, starch is rendered soluble, and is converted into Nasse's *amidulin*, which still turns blue with iodine. On longer boiling it undergoes a further change into *erythrodextrin*, or ordinary dextrin, which colours red with iodine; and after a still longer time it becomes converted into another kind of dextrin, *achroodextrin*, which tastes sweet and does not colour with iodine, and into a kind of sugar termed *glycose* (starch sugar, dextrose sugar, grape sugar). All

* "Leçons," 1859, vol. ii. p. 112.

† "Archiv f. Path. Anat." x. p. 140.

the above-mentioned bodies rotate the plane of polarization to the right. Its maximum rotating power is 103·14, the minimum 56·7.* Changes essentially similar to those just described as produced in starch by boiling with acid are effected by the action of a ferment termed diastase, which is developed in germinating seeds. Diastase breaks up starch into glycose and achroodextrin, and if fermentation continues the latter is gradually almost wholly converted into glycose.† According to MM. Musculus and Gruber‡ starch is a polysaccharide, having the formula $(C_{12}H_{20}O_{10})n$, in which n has a value of 5 or 6. When acted on by diastase and boiling dilute sulphuric acid, starch forms or breaks up successively into soluble starch; erythrodextrin; α, β, and γ, achroodextrin; maltose, and glycose. At each decomposition maltose is formed and a new dextrin of feebler molecular weight, n becoming less and less till achroodextrin γ is formed, which is probably converted into maltose by simple hydration. Maltose in its turn is disintegrated into two molecules of glycose, $C_{12}H_{22}O_{11} + H_2O$ (Maltose) $= 2(C_6H_{12}O_6)$ (Glycose). Starch constitutes an important article of diet.

Cane Sugar, $C_{12}H_{22}O_{11}$, though largely consumed as food, does not form a part of the healthy body. It forms 88 per cent. of the juice of the sugar cane, and is also obtained from beetroot. The crystals are modified monoclinic prisms, and dissolve in one-third of their weight of water, and less easily in alcohol. On boiling with water cane sugar is converted into invert sugar, or fruit sugar, which is a mixture of levulose and dextrose, and rotates to the left on account of the superior rotatory power of levulose. It appears to be converted into grape sugar partly by the action of a ferment contained in the mucin secreted by the stomach, partly by the pancreatic and intestinal juices; milk sugar as well as grape sugar probably both undergo direct absorption into the veins,§ with comparatively little change, except that a part seems to be converted into lactic acid and butyric acid.

Dextrose, or Grape Sugar, $C_6H_{12}O_6 + H_2O$, crystallizes in warty masses which are found under the microscope to consist of rhombic tablets. It is soluble in cold, and very soluble in hot water and in alcohol, but not in ether. It is capable of two kinds of fermentation—alcoholic, induced by yeast, and lactic, accompanied by the growth of a protophyte, and it is especially characterized by its power of reducing all easily reducible metallic oxides, as those of copper, bismuth, tungsten, and molybdenum in alkaline solutions. It occurs naturally in the alimentary canal as the product of the conversion of starch into sugar through the action of the salivary, pancreatic, and intestinal juices, and from thence by absorption it gains entrance into the chyle and blood. It exists in small quantities in the egg of the bird, in the amniotic and allantoic fluids of the herbivora, and occasionally in the urine of man. It is the chief or only saccharine constituent of the urine in diabetes, and it may also be made to appear in the urine by injury of the medulla oblongata.

Tests for Grape Sugar.—1. An alkaline solution reduces copper oxide to suboxide (*Trommer's Test*). 2. An alkaline solution also reduces bismuth oxide to bismuth suboxide which is black (*Böttcher's Test*). 3. Boiled with solution of potash it becomes brown, and on addition of nitric acid evolves an odour of caramel (*Moore and Heller's Test*). 4. Indigo carmine solution and sodium carbonate give with sugar solution on heating a play of colours—green, purple, red, yellow (*Mulder and Neubauer's Test*). 5. Sugar evaporated to dryness with H_2SO_3, or HCl, leaves a black shiny residue (*Runge and Reich's Test*). 6. Grape sugar boiled with silver nitrate and ammonia deposits metallic silver.

* Béchamp, "Rev. Scient." 1877-1878, p. 427. † See Brücke, Vorlesungen, 1874, p. 221.
‡ v. Mering, "Archiv f. Anat. v. Physiol." 1877, p. 379.
§ "Compt. Rend. de l'Acad. des Science," June 10, 1878.

7. Alcoholic solution of grape sugar mixed with alcoholic solution of caustic potash gives a white flocculent precipitate of grape sugar and potassium. 8. The Fermentation Test. 9. On boiling with a mixture of cupric sulphate and potassium sodium tartrate dissolved in caustic soda (Fehling's solution) the copper is reduced.

Lactose, or Milk Sugar, $C_{12}H_{22}O_{11} + H_2O$, exists in the proportion of from 3 to 5 or 6 per cent. in the milk of various animals. It is feebly saccharine to the taste, and is gritty to the teeth, and is less soluble than dextrose. Like grape sugar it reduces the salts of copper in an alkaline solution, and rotates the plane of polarization to the right. Lactose undergoes lactic, but not readily alcoholic fermentation.

Glycogen, $C_6H_{10}O_5$ (*Liver Sugar*).—This remarkable substance was first obtained by C. Bernard by immersing the livers of various animals, within a few seconds of their death, in boiling water, to coagulate the albumen, then bruising the mass in a mortar and filtering the liquid through animal charcoal. On the addition of alcohol in excess or of glacial acetic acid, the glycogen is precipitated as a white and tasteless amorphous material soluble in water, and then forming an opalescent solution, but incapable of effecting the reduction of the salts of copper. Brücke* has lately recommended the double iodide of mercury and potassium as the best means of completely precipitating pure glycogen. The solution is prepared by precipitating solution of corrosive sublimate with potassium iodide, washing the precipitate and dissolving it in hot solution of potassium iodide till the latter is saturated with it. Pure glycogen may now be obtained by first placing the liver in boiling water, then bruising it in a mortar, returning it to the same water, and boiling it for ten minutes; filtering and rapidly cooling the solution with ice or a refrigerator. Hydrochloric acid and the mercurial solution are then alternately added as long as any precipitate falls, the fluid is filtered and alcohol added to the filtrate till an abundant precipitate of glycogen takes place. This is washed successively with weak alcohol, strong alcohol, and absolute alcohol, and finally purified with ether. Glycogen thus obtained is free from nitrogen and leaves no ash when burnt. It is coloured red with iodine, not brown. Under the action of dilute acids, with the exception of nitric acid, glycogen is converted into dextrose, and the same effect is produced with all amylolytic ferments, as ptyalin and amylopsin. It rotates the plane of polarization to the right. Glycogen has been found to be constantly present in the muscles, in all embryonic tissues, in the placenta, testes, brain, and white blood corpuscles; in the notochord, and in cartilage, whether hyaline, fibrous, or elastic,† but only very small traces of a substance, the identity of which with glycogen was somewhat doubtful, can be obtained from the blood, spleen, kidneys, or secreting mammary gland, so that it can scarcely be admitted that it is stored up in the body as a preliminary stage of the formation of milk sugar. All muscles yield sugar, part of which appears to present identity of composition with grape and liver sugar, whilst part possesses distinctive characters, and has received the name of Inosit. Weiss‡ found that muscular activity was associated with a marked decrease in the per-centage of glycogen in the case of frogs, amounting to a quarter of the total normal quantity. The heart, however, in spite of its constant activity, contains (in the dog) two-thirds as much glycogen as ordinary muscular flesh.

Inosit (*Muscle Sugar*), $C_6H_{12}O_6 + 2H_2O$, is a kind of sugar which was originally found in the expressed muscle juice of the heart;§ but exists also in the pancreas and thymus glands; in the lungs, kidneys, liver, and spleen;‖ in the brain¶ and

* "Wien Akad. Ber." Band lxiii. Feb. 1873. † Neumann, "Archiv f. Mik. Anat." Heft 1.
‡ "Wien Akad. Ber." Band lxiv.ii. § Scherer, "Ann. Chem. u. Pharm." Band lxxiii. p. 322.
‖ "Cloetta, Vierteljahr. der Nat.-For. Gesells. in Zürich," Band i. p. 205.
¶ Müller, ibid., Band ciii. p. 140.

suprarenal capsules of the ox. In disease, as in diabetes and Bright's disease, it occurs in the urine. It is identical with the Phaseomannite found in beans, and it is found elsewhere in the vegetable kingdom. It crystallizes in long rhomobhedra, which are at first transparent, but subsequently become opaque. It possesses a feebly saccharine taste, and has no power of rotating the plane of polarized light; nor does it, like some other kinds of sugar, reduce the salts of bismuth, copper, or silver in an alkaline solution. A good test for it, suggested by Scherer, consists in heating to dryness the supposed mass with a little nitric acid in a porcelain dish, then moistening it with chloride of calcium, and again evaporating it, when a rose-red mass remains. It does not undergo alcoholic fermentation, but when in contact with decomposing albuminous bodies it yields lactic and butyric acids; or, according to Helger,* sarcolactic acid. The experiment of tetanizing an animal for a considerable period of time, performed by P. Spiro,† shows that after prolonged muscular exertion sarcolactic acid, probably derived from the decomposition of inosite, is contained in considerable quantities in the blood.

Chondroglycose.—This form of sugar is obtained from chondrin when it is exposed to concentrated and boiling hydrochloric acid, or to the influence of gastric digestion. It crystallizes with difficulty, rotates the plane of polarized light to the left ($-46°{\cdot}5$), and is only partially capable of undergoing fermentation, a part refusing to ferment; and the solution after fermentation only rotating polarized light to half the extent. Chrondroglycose forms an easily soluble combination with lime.

Formic Acid, CH_2O_2.—This is a colourless fluid with peculiar odour, crystallizing below 0° C. The vapour is combustible, and highly irritating (raising a blister when applied to the skin). Heated with concentrated sulphuric acid it yields carbonic oxide and water. Iron chloride gives a blood-red colour with solutions of its salts. The acid is free or combined with bases in ants, in the stings and poisonous secretions of various insects, and in the stinging hairs of the procession caterpillar; in the sweat; in the juice of the spleen, pancreas, and thymus; in muscle juice; in the brain; in the blood in leukæmia, and in the urine. Formic acid is generally a product of the disintegration of organic bodies, as of the albuminoids, whilst it also results from the action of ozone on glycerine, the fats, and fatty acids. It is probably one of the final products of the disintegration of the albuminous compounds in the animal body.

Acetic Acid, $C_2H_4O_2$.—A colourless, pleasant-smelling, inflammable fluid, having when concentrated a sp. gr. of 1·063, crystallizing at 5° C., boiling at 119° C. When distilled with strong bases it furnishes acetone. Nitrate of silver added to solutions of neutral acetates gives a white crystalline precipitate soluble in ammonia. Like formic acid, it is one of the final products of the metabolism of the albuminoid compounds. It has been found in the sweat, in the juice of muscles, of the spleen and other glands, and in the blood of leukæmic patients; also in the blood of animals the food of which has been saturated with brandy, and sometimes in the stomach after the use of much saccharine or amylaceous food.

Lactic Acid, $C_3H_6O_3$.—Of this acid there are two isomeric modifications—fermentation, or ethidene lactic acid, and β-lactic or ethene lactic acid, which last is of little interest to the physiologist.

Ethidene lactic acid, called *isolactic* and *fermentation lactic acid*, is the ordinary lactic acid produced by a peculiar fermentation of sugar and other carbohydrates, which occurs at temperatures between 20° and 40° C. (58°—104° F.), and requires the presence of water and certain ferments—viz., albuminous substances in a peculiar state of decomposition, such as casein, glutin, or animal

* Müller, ibid., Band clx. p. 333. † "Zeits. f. Physiol. Chemie," 1878, Band i. p. 111

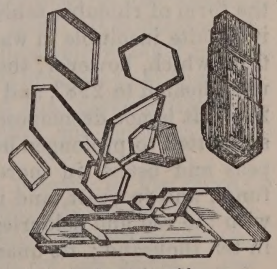
membranes, especially the mucous membrane of the stomach of the calf (rennet) or of the dog, or bladder. According to Pasteur, it depends on the presence of a peculiar fungus—the *Penicillium glaucum*. In its most concentrated condition it is a strongly acid, tasteless and odourless syrupy fluid, which under certain conditions gelatinizes. Its sp. gr. is 1·215. It is readily soluble in all proportions in water, ether, and alcohol. It is not volatile, and expels volatile and some mineral acids from their combinations at high temperatures. It breaks up into carbonic acid and carbonic oxide gases, aldehyde, and other compounds. When placed in contact with decomposing animal substances it decomposes into butyric acid, carbonic acid gas, and hydrogen.

Sarcolactic acid, or *paralactic acid*, is a form of lactic acid existing in the animal organism, especially in muscle, from which it may be extracted by cold water or dilute alcohol. It is most easily prepared from Liebig's extract of meat. It agrees in all its reactions with fermentation lactic acid, and must therefore be an ethidene-lactic acid, but differs from it in rotating the plane of polarization to the left, whereas ordinary lactic acid is optically inactive. Lactic acid, either free or in combination, is widely distributed in the body. Fermentation lactic acid, for example, has been found in the gastric juice, in the contents of the small and large intestine, and in the chyle of the thoracic duct of horses after abundant amyloid food; whilst sarcolactic acid exists in the juice of both striated and unstriated muscle in ox-gall, and in the fluid of ovarian cysts. Lactic acid, though of which form has not been determined, is found in the juice of the spleen, liver, thymus, thyroid, pancreas, lungs, and brain; as a sodium salt in the allantoic fluid of the cow, and as a calcium salt in the urine of the horse. It is also found in many pathological conditions, as in the milk if too long retained, in the blood in leukæmia, pyæmia, and puerperal fever, in purulent extravasations, in the urine of patients suffering from rachitis and osteomalacia, and trichinosis, and especially from acute atrophy of the liver in poisoning by phosphorus; in the latter two cases probably in the form of sarcolactic acid. It has also been noticed in the saliva in diabetes, and in the sweat in puerperal fever. The lactic acid found in the body proceeds then from two sources—from fermentative changes in the food, and from regressive metamorphosis taking place in the tissues, and in the case of muscle, of the sugar it contains.

Glycerin-phosphoric Acid, $C_3H_5(OH_2).O.PO(OH)_2$.—This acid may be prepared by gradually adding powdered metaphosphoric acid to cooled glycerin. Combination takes place with considerable elevation of temperature. It may also be obtained from the yolk of egg. It forms a sour syrupy liquid, which breaks up at a moderately high temperature into glycerin and phosphoric acid.

Succinic Acid, $C_4H_6O_4$.—A very stable organic acid, crystallizing in rhombic prisms and rhombohedric plates; it is tasteless, and dissolves easily in water. It occurs in the parenchymatous juices of the spleen, thymus, and thyroid glands of the ox, in the urine of the herbivora, in the contents of cysts containing echinococci in man, in the fluid of hydrocele, in cases of hydrocephalus, and in considerable quantity in the blood of the rabbit, goat, ox, and horse. It appears to belong to a series of acids obtained by the action of powerful oxydizing agents on fats, and is one of the terminal products of their disintegration. It can be obtained from the oxidation of butyric acid, malic acid, and asparagin, to the use of which last substance its occurrence in the urine is probably usually due.

Fig. 62.



Succinic acid.

Oxalic Acid, $C_2O_2(OH_2)$, is frequently found in urine after the use of certain kinds of vegetable food. In combination with lime it constitutes a formidable variety of calculus. It is a constantly-occurring product of the oxidation of organic bodies, and stands in close relation with uric acid.

59. Oleaginous Compounds.—The animal fats are glycerides, *i.e.*, compound ethers of the trivalent alcohol glycerin and the fatty acids. Those usually present are tripalmitin, tristearin, and triolein, which are represented by the formula:—

Tristearin (Tristearic Acid Glyceride) $\left.\begin{matrix}(C_{18}H_{35}O)_3\\C_3H_5\end{matrix}\right\}O_3$

Tripalmitin (Tripalmitinic Acid Glyceride) $\left.\begin{matrix}(C_{16}H_{31}O)_3\\C_3H_5\end{matrix}\right\}O_3$

Triolein (Triolinic Acid Glyceride) $\left.\begin{matrix}(C_{18}H_{33}O)_3\\C_3H_5\end{matrix}\right\}O_3$

These are associated in human fat in the proportion of about three-fourths of stearin and palmitin and one-fourth of olein. The mean per-centage composition of human fat is C 76·62, H 11·94, O 11·44, expressed by the empirical formula $C_{62}H_{99}O_6$. The substance formerly called margarin is a mixture of tripalmitin and tristearin. A separation of these proximate principles within the cells may occasionally be observed at low temperatures; the more solid fats, tripalmitin and tristearin, appearing as a minute stella of crystalline form, surrounded by the still fluid triolein. Exposed to the action of superheated steam they break up into the fatty acids and glycerin. All the animal fats are soluble in hot alcohol, in ether, fluid oils, benzole, carbon disulphide, and in chloroform. They are distinguished from one another by the temperature at which they respectively solidify, and by the salts that they form with the alkalies.

The following Table shows about the proportion in which they are found in some of the fluids and tissues of the body:—

	Per-centage of fat.		Per-centage of fat.		Per-centage of fat.
Sweat	0·001	Blood	0·4	Milk	4·3
Vitreous Humour	0·002	Cartilage	1·3	Cortex of Brain	5·5
Saliva	0·02	Bone	1·4	Brain (whole)	8·0
Lymph	0·05	Bile	1·4	Hen's Egg	11·6
Synovia	0·06	Crystalline Lens	2·	Medulla of brain	20·
Liq. Amnii	0·06	Liver	2·4	Nerves	22·1
Chyle	0·2	Muscles	3·3	Spinal Cord	23·6
Mucus	0·3	Hair	4·2	Adipose Tissue	82·7

Cholesterin, $\left.\begin{matrix}C_{26}H_{43}\\H\end{matrix}\right\}O + H_2O$ (or *biliary fat*), is a hard, spermaceti-like substance, constituting the greater part of gall-stones, and separating from its solutions in nacreous scales that are found under the microscope to have the form of rhombic tablets, the obtuse angle being 100° 30′, the acute 79° 30′: it is quite insoluble in water, but is soluble in ether, and also in boiling alcohol, from which, however, the greater part separates on cooling. It does not melt until heated to 298°, and it solidifies again and becomes perfectly crystalline at 275°. It is not decomposed by concentrated alkalies even when the mixture is submitted to prolonged heat. It is widely distributed in plants,* being found in peas and beans, in increasing amount as they ripen, in young rosebuds, in fungi, and in yeast, and is constantly present in the blood (chiefly in association with the red and colourless corpuscles) in the proportion of about two parts in ten thousand; its quantity seems to be augmented in old age. It is found

* Beneke, "Annalen Chem. Pharm." Band cxxii. p. 249, and cxxvii. p. 105. Ritthausen, "Chem. Centralblatt," 1863, p. 500. Hoppe-Seyler, "Physiologische Chemie," 1877, p. 81. Lindenmeyer, "Beiträge zur Kenntniss des Cholesterins, Inaug. Dissert." 1863.

also in the bile, in lymph and meconium, the spleen, and in most glands, in the yolk of egg and in spermatozoa, and is stated to be a constituent of the nervous tissue, being probably a product of the disintegration of the nerve substance. It is frequently separated from the blood as a morbid product; thus it is often present in considerable quantity in dropsical fluids, and particularly in the contents of cysts. It is occasionally seen in disorganized eyes, floating in detached scales in the fluid vitreous, and is sometimes deposited in the solid form in degenerated structures, tubercular concretions, &c. It is not present in the fæces, except after long fasting, being normally converted into stercorin as it passes down the intestine. Strong arguments have been adduced by Dr. Austin Flint* for regarding it as an excrementitious principle discharged by the liver, and hardly second in importance to urea. He has found it always more abundant in the blood returning from the brain than elsewhere; also that its quantity is exceedingly small in the venous blood of the paralysed side in hemiplegia; and that in cases of serious structural disease of the liver, accompanied by symptoms pointing to blood-poisoning, cholesterin accumulates in the blood, constituting a condition which he has called Cholesteræmia.

Valerianic Acid, $C_5H_{10}O_2$.—A colourless oily fluid, of penetrating cheesy odour and pungent taste. It forms an oily spot on paper, which disappears on being heated; when concentrated it is inflammable. It is readily soluble in alcohol and ether, but requires 30 volumes of water for solution. It boils at 175° C., but remains fluid at −15° C. Neither this acid nor capronic acid, $C_6H_{12}O_2$, caprylic acid, $C_8H_{16}O_2$, nor capronic acid, $C_{10}H_{20}O_2$, have been shown to be certainly present under physiological conditions in the body, though it is not improbable that one or more of them may be found in the sweat and in the blood.

Propionic Acid, $C_2H_6O_2$, when concentrated is an oily colourless fluid, crystallizing in laminæ at a low temperature, and boiling at about 140° C. It has a peculiar smell and a burning taste. It is doubtful whether it forms a constituent of the animal organism, though it may probably exist in the juices of some glands and in the blood in leukæmia. Its artificial production by oxidation of the albuminous compounds and of the fatty acids, is in favour of this view. Von Gorup Besanez† states that he has obtained it as a product of the oxidation of glycerin by ozone in an alkaline solution. Schottin believes it to be present in the sweat, and C. Schmidt in the gastric juice.

Butyric Acid, $C_4H_8O_2$.—An oily colourless fluid, smelling strongly of rancid butter, with pungent taste; sp. gr. 0·97; boils at 157° C.; remains solid even at −20° C.; burns with a blue flame. Its combinations with alkalies are volatile and non-crystallizable. It has been found in the sweat, in the juice of muscles, of the spleen and other glands, occasionally in the urine, in the contents of the stomach, and in vomited matter, in the contents of the cæcum, and in the solid excrement after the use of vegetable food. It is discharged by some beetles of the genus Carabus. It has not been certainly found in the blood. Its occurrence in the alimentary canal is attributable to changes in the constituents of the food, especially as it is known that carbohydrates in presence of organised ferments constantly undergo butyric and lactic acid fermentation.

Phenol.—Traces of this substance are constantly present in the fæces.‡ Like Indol, it appears as one of the products of the changes occurring when albuminous substances and the pancreas are undergoing putrefactive decomposition.§ The incarceration of a portion of intestine, or the arrest of the

* "Physiology of Man," vol. ii. p. 402. † "Physiolog. Chemie." 1874, p. 296.
‡ Brieger, "Ber. d. Deutsch. Chem. Gesellschaft," Band x. p. 1027, 1877.
§ Baumann, "Zeits. f. Physiol. Chemie," Band i. p. 60, 1877.

onward movement and absorption of the contents of the intestine, if these are rich in proteids, leads to the appearance of phenyl-sulphuric acid in the urine.* The mode in which it arises, however, whether as a simple product of decomposition of albumen with absorption of water, or as a reduction process, is unknown.

Skatol, C_9H_9N.—This, like Indol, is one of the products of the disintegration of albumen. It is obtained in the form of shining laminæ, melting at 95° C., by washing fæces with a solution of acetic acid and distilling. The distillate is neutralized with sodium carbonate, and shaken with ether. After evaporation of the ether, the residue is boiled with hot water, from which on cooling skatol is deposited.† It is to this substance that the odour of the fæces appears to be chiefly due.

Stercorin.—This term has been applied by Dr. Austin Flint to a peculiar substance, crystallizing in needles, which may be extracted from normal fæces by the successive action of ether, alcohol, and a hot solution of caustic potash, by which all the saponifiable fats are removed. On largely diluting the mixture with water, filtering, acting on the residue with ether and alcohol, and evaporating, pure stercorin may be obtained. It resembles cholesterin in many points, and is believed to proceed from that substance. Its crystalline form is, however, different, and it fuses at a lower temperature—96°·8 Fahr. About ten grains are eliminated per diem.

60. Inorganic Compounds.—The principal inorganic compounds that form part of the tissues and fluids of the body are water carbonic acid, and ammonia; the carbonates, chlorides, sulphates, and phosphates of the alkalies and alkaline earths, and potassium sulpho-cyanide. *Water* is the most widely distributed of all the constituents of the body, and forms rather more than half its weight (59 per cent.), the different tissues, however, containing very various amounts, from the enamel of the teeth, which has only 2 per 1000, to the renal tissue, which has 827 per 1000. Fat contains 209 per 1000; the tissues of the liver, 693; of the spinal cord, 697; of the skin, 720; of the brain, 750; of the muscles, 757; of the spleen, 758; of the thymus, 770; of the nerves, 780; and the heart, 792 parts in 1000. It is for the most part directly ingested, but a small portion is probably also formed in the body, as one of the terminal products of the various chemical changes undergone by the more complex substances used as food. It is discharged from the body by the kidneys, skin, lungs and bowels. It confers elasticity, extensibility, and translucency on the several tissues. It is a general solvent, and is essential for all processes of imbibition, diffusion, and of movement in general, both in a chemical and physical sense. By its evaporation, a large amount of heat is rendered latent, and it hence serves as the chief heat regulator of the body. The physiological significance of the various *saline constituents*, except in so far as they form part of the bony skeleton, has not been satisfactorily ascertained, though in some instances it is probable they serve to retain in solution some of the organic compounds. With the exception of common salt, they are rarely taken into the body in their chemically pure state, being usually combined with the organic constituents of the food, and are not less important than these in the general processes of nutrition. In some few instances they appear to be formed in the body, as in the case of the alkaline sulphates and phosphates, the former of which, whilst partially consumed with the food, are in part derived from the oxidation of the sulphur contained in the albuminous compounds, whilst the latter in part proceed from the oxidation

* Salkowski, "Ber. d. Deutsch. Chem. Gesellschaft," Band ix. p. 1595, 1876.
† Nencki, "Centralblatt für die Med. Wiss,' 1878, p. 849.

of phosphorus in organic compounds. The salts ingested are eliminated for the most part unaltered by the kidneys and bowels. The chief exceptions to this rule are found in the salts of the vegetable acids as the tartrates, malates, and citrates, which undergo decomposition in the blood, and are discharged in the condition of carbonates. The most widely-distributed, as well as perhaps the most important salt in the body is *sodium-chloride*, or *common salt*. The blood contains rather more than 4 parts of it in 1000, and the proportion undergoes but little variation, whether an excess or a deficiency be ingested with the food—in the one case the superfluous quantity being quickly eliminated by the urine, and in the other, the system retaining its hold of the salt with such pertinacity that the quantity discharged falls to a minimum, or its elimination is altogether arrested. Dr. Broadbent* has pointed out that this retention can only be in virtue of a special chemical relation between the salt and the animal tissues and fluids, and it is in consequence of such affinity that it, as well as other salts, are of service in the organic processes. It is present in considerable quantity in chyle, lymph, and white of eggs; in the salivary and gastric fluids; in mucus, pus, and inflammatory exudates; whilst it is remarkably deficient in the yolk of eggs, in the juice of muscles, and in the secretion of some glands. Its uses are numerous. It exerts an important influence on all the diffusion processes that take place in the body, affecting in this way the absorption and interchange of material; whilst by conferring, in association with other salts, a certain density upon the blood plasma, it plays an important part in the conservation of the morphological elements of the blood in their natural condition. It also seems to be essential to the performance of many of the metamorphic and histogenetic operations to which the organic constituents of the food are subjected in the animal economy. It was demonstrated by Boussingault,† that when, of two sets of oxen, one was allowed the unrestricted use of salt, whilst the other was as far as possible deprived of its use, a marked contrast was observable in the course of a few weeks between them, and manifestly to the advantage of the former. The desire for common salt on the part of animals and man is extremely powerful, leading the former, especially if they be vegetable feeders, to traverse great distances to reach saline deposits: whilst strong evidence of the necessity for its use in man is afforded by the fact mentioned by Brücke, that many military deserters who live a wild life in the mountains of Salzburg, Upper Australia, and Carinthia, risk their liberty and even lives to obtain it in town or village. Its importance is also shown by the circumstance,‡ that if salt be completely excluded from the food for three days, albumen appears in the urine. *Disodium orthophosphate* (Na_2HPO_4) and sodium *carbonate*, the latter of which is partly ingested with the food, and partly results from the decomposition of the salts of malic, citric, and tartaric acids, would seem to have as their chief purpose the maintenance of the alkalinity of the blood, on which depends not merely the solubility of its albumen, but the facility of its passage through the capillaries, and the readiness with which its combustive materials are oxidized, whilst they also increase the absorptive power of the liquor sanguinis for gases, and thus play an important part in the respiratory process. The salts of *potash* appear to be specially required for the nutrition of the muscles and nerves, since they are largely present in the fluids and ashes of those tissues, but they probably exert the same general influence as those of soda. The quantity present in the

* "An Attempt to apply Chemical Principles in Explanation of the Action of Remedies and Poisons." 1869.

† "Mémoire de Chemie Agricole," 1854, p. 271.

‡ Jaccoud, "Nouv. Dict. d. Sci. Med." vol. i. p. 536.

blood cannot exceed certain limits, since the observations of Grandeau and others* have shown that the injection of potassium salts, and especially of potassium chloride, are even in dilute solution highly poisonous, paralysing the heart and striated muscles. It is remarkable that when injected into the stomach the action of potassium chloride is different, increasing the frequency and force of the heart's action, and the pressure of the blood.† The presence of the earthy salts, on the other hand, would seem to have reference almost exclusively to the composition of the tissues, into which some of them enter very largely. *Calcium phosphate*, in particular, must be regarded almost in the light of a histogenetic substance so constantly is it present in newly-forming tissues, whilst it is also in great demand as the principal consolidating material of bone and tooth. Whether the *calcium carbonate*, *magnesium phosphate*, the *calcium fluoride*, and the *silica* of the blood, are of any other use than to supply consolidating materials for the tissues, there is at present no evidence whatever. *Iron*, like the alkaline salts, is an essential constituent of the blood itself, forming a large per-centage of the hæmoglobin of its red corpuscles, and it is supplied by the blood to various tissues, especially the muscles and the hair, of which also it may be considered an essential component. Estimating the quantity of blood with Bischoff (highly) at 7·7 per cent. of the whole weight of the body, the total quantity of iron contained in the blood of a man, weighing about 150 lbs., would be 45 grains. The normal proportions of all these substances are essentially maintained by means of the excretory apparatus, which filters off (so to speak) any surplus, it being through the urinary organs that they are chiefly eliminated. And it is by them, too, that the normal proportion of water in the blood is maintained; the Malpighian apparatus of the kidneys apparently acting as a kind of safety valve, through which any surplus that remains after the cutaneous, pulmonary, and intestinal exhalants have performed their appropriate duties, is allowed to make its escape.

CHAPTER V.

OF FOOD, AND THE DIGESTIVE PROCESS.

1. *Of Food, its Nature and Destination.*

61. From the foregoing observations regarding the composition of the tissues and fluids of the body, it may be concluded that the substances which are required by animals for the development and maintenance of their fabric are of two kinds, the Organic and the Inorganic. The Organic alone are commonly reckoned as aliments: but the latter are really not less requisite for the sustenance of the body, which speedily disintegrates if the attempt be made to support it upon any Organic compounds in a state of purity. In all ordinary articles of diet, however, the Inorganic matters are present in the requisite proportion; and hence it is that the necessity which exists for their employment has very commonly escaped notice.

62. The Organic compounds usually employed as food by Man are partly derived from the Animal, and partly from the Vegetable Kingdom; and they may be conveniently arranged under the three heads already mentioned of the Saccharine, the Oleaginous, and the Albuminous—under which last

* Traube, Bernard, Ranke, Podcapäw, and Guttmann.
† Kemmerich, "Archiv f. Phys." Band ii. p. 49.

gelatine is included. There are many other substances, however, which, though truly alimentary and consumed to a considerable amount, cannot be legitimately placed under either of the above heads—such are, for example, the vegetable acids, and pectine, or vegetable jelly. The compounds belonging to the *Saccharine* group consumed as food, though existing in small proportions in the animal tissues and fluids, are principally derived from the vegetable kingdom, in which they are frequently present to a large amount. It is probable that cane-sugar undergoes conversion into a special form of sugar either at the liver or soon after it has entered the blood. Starch is for the most part converted into amidulin, erythrodextrin, achroodextrin, dextrin, and a peculiar form of sugar; and by a further process of oxidation or combustion after absorption these compounds generate carbonic acid, which is chiefly eliminated by the lungs, and thus become directly subservient to the generation of nervo-muscular force, and to the maintenance of the heat of the body. That the saccharine substances are *per se* insufficient for the maintenance of life has been shown by numerous experiments upon animals, and by the interesting experiments of Dr. Hammond,* who on one occasion limited himself to a diet of 1½ lb. of gum per diem, and on another to a similar quantity of starch and water. In both sets of experiments hunger, debility, and febrile excitement were soon experienced, and he was finally compelled to discontinue the gum diet on the fourth day, though he was able to persevere in the use of the starch till the tenth—a circumstance which was probably partly due to its still retaining a small proportion of gluten, and partly to its not producing such serious disorder of the stomach and bowels as the gum.

63. The *Oleaginous* compounds (§ 59) which enter so largely into the composition of the body,—being not only stored up in masses in the adipose substance, but also forming constant and important constituents of the muscular, nervous, and other tissues,—are partly introduced into the system from without, and are also partly the result of the chemical metamorphoses effected within the body upon the albuminous and saccharine compounds: by which means the latter become subservient to the nutrition of the several nitrogenous as well as non-nitrogenous tissues. In the diet of the Carnivora, the fats almost entirely replace the carbohydrates consumed by the Herbivora. Previous to absorption the oleaginous substances undergo fine division, and, perhaps, to some extent saponification; whilst after their entrance into the circulation they are partly applied to the purposes of nutrition, partly to the production of nervo-muscular force, and partly, there is good reason for believing, combine immediately with oxygen, and thus support the animal heat. Like the saccharine, the oleaginous compounds when consumed alone are wholly incapable of supporting life; and the only benefit that a starving animal obtains from their consumption is the maintenance of its temperature, and a consequent slight prolongation of its life; death occurring, as has been shown by Mr. Savory, when non-nitrogenous food is freely supplied,† not from loss of temperature, as in inanition, but from loss of tissue. The experiments of Dr. Ed. Smith on the elimination of carbonic acid, and of MM. Fick and Wislicenus, and Dr. Parkes, on the excretion of nitrogen during rest and exercise, as well as the more theoretical considerations adduced by Professor Frankland, alike tend to show that during the period of active exertion the nitrogen-holding substance of the muscles undergoes comparatively trifling increase in the disintegration to which it is constantly sub-

* "Experimental Researches on Food," Philadelphia, 1857.

† "Proceedings of Royal Society," May 1, 1862.

ject, whilst a marked increase occurs in the oxidation of the hydrocarbonaceous constituents; the union of these with oxygen, or their combustion, appearing to generate the force which is rendered apparent in locomotion or manual labour. Hence it is found that considerable, and with healthy muscles even prolonged, exertion can be made on food containing little or no nitrogen —as, for instance, on biscuits made of starch and sugar, or starch and fat. General experience, however, as well as the experiments of Dr. Hammond and Mr. Savory—as we have already seen—and especially those of Dr. Parkes, which will hereafter be more fully discussed, show conclusively that there is a limit to the muscular force which can be exerted under such circumstances; and that when food has been administered which is either altogether deficient in nitrogen, or which contains an insufficient supply of that substance, sooner or later the power of the muscles diminishes, and at length altogether fails. It may therefore be regarded as a well-established fact that when severe and sustained muscular exertion is required to be performed, the food must contain not only a due supply of hydrocarbonaceous and easily oxidizable substance which may develop the muscular force, but also a sufficient amount of nitrogenous material to repair the waste of tissue which occurs in the act of contraction.

64. The substances forming the *Albuminous* group (§ 56) are applicable to the support of the Animal body, both by affording the materials for the nutrition and re-formation of its tissues, and also by serving for the maintenance of its heat, and the production of muscular force, through the decomposition of which they are susceptible, into hydrocarbonaceous matters capable of undergoing direct oxidation, and highly-azotized compounds which ultimately pass-off by the kidneys. The proportions of carbon, hydrogen, oxygen, and nitrogen, of which all these substances are composed, appear to be very similar; and they seem all capable of being reduced by the digestive process to a like condition. Hence it is a matter of little consequence, except as regards their digestibility and the proportion of inorganic matters with which they may be respectively united, whether we draw our histogenetic materials from the flesh of animals (myosin, syntonin), from the white of egg (albumen), from the curd of milk (casein), from the grain of wheat (gluten), or from the seed of the pea or bean (legumin). Neither of these substances, however, can long sustain life when it is used by itself; for it has been experimentally ascertained, that by being made to feed constantly on the same substance (boiled white-of-egg, for instance, or meat deprived of the osmazome that gives it flavour), an animal may be effectually starved; its disgust at such food being such, that even if this be swallowed, it is not digested. Thus Dr. Hammond limited himself for a period of ten days to a diet of about 1½ lb. of albumen obtained from the serum of bullock's blood, and 4 lbs. of distilled water per diem. Little inconvenience was experienced until the fourth day, when loss of appetite, headache, and debility were felt. The severity of these symptoms rapidly increased, and the disgust which the monotony of the diet occasioned was so great, that it was with much difficulty the albumen could be eaten. On the seventh day, albumen appeared in the urine; and on the ninth, such severe diarrhœa set in that he was compelled to give up the experiment. There was no failure in the maintenance of the temperature of the body, though its weight was notably diminished at the end of the experiment, and the mental faculties remained clear throughout.—The value of *gelatin* as a food, nearly allied as it is to the albuminous compounds, seems to be small, and it certainly cannot permanently replace albumen as an article of diet. The nutritive value of soups and broths are probably chiefly attributable to the albuminous

matters which they hold in solution, though it may also in some measure be due to the readiness with which their gelatinous constituents can be absorbed and applied to the purposes of nutrition and calorification. The very large quantity of gelatin which Bischoff and Voit found it necessary to make their dog consume in order to maintain its weight,—a quantity of *dry* gelatin, in fact, equal to the weight of moist flesh on which the animal was ordinarily fed,—is worthy of particular notice, and indicates either that little is absorbed, or that when absorbed it is not readily applied to the nutrition of the tissues. When consumed in large quantities it increases the specific gravity of the urine and the amount of urea it contains.* It is very interesting to remark (with Dr. Prout) that, in the only instance in which Nature has provided a *single* article of food for the support of the animal body, she has mingled articles from all the preceding groups. This is the case in *Milk*, which contains of salts nearly equal proportions; of albuminous substance, *casein*, which forms its curd; of *oily* matter, the butter; and of *sugar*, which is dissolved in the whey. The proportions of these vary in the milk of different Mammalia, and they depend in part upon the nature of the food supplied to the Animal that forms the milk; but the substances are thus combined in every instance.

65. It is, however, impossible to measure the value of any particular kind of food for either purpose by a consideration merely of its ultimate or even of its proximate constitution; since its fitness as an article of diet will also depend upon the facility with which it may be reduced by the digestive process, and afterwards assimilated. Thus an aliment abounding in nutritive matter may be inferior to one which really contains a much smaller proportion, if only a part in the first case, and the whole in the second, be readily taken-up by the system. It is obvious that the most *economical* diet will be that in which there is the most perfect apportionment of the several classes of constituents to the wants of the system; and these will vary with the amount of muscular exertion put forth, and with the elevation or depression of the external temperature. Thus, for a man of ordinary habits, and living under a medium temperature, a diet composed of either bread or of animal flesh alone is far from being the most economical. No doubt there are particular conditions of existence under which life may be advantageously supported upon *animal* food alone. Thus the Guachos of South America, who pass the

* Bischoff and Voit, "Gesetze der Ernährung," 1860, p. 215; and see the Report of the French "Gelatine Commission," in the "Compt. Rend.' Août, 1841; that of the Amsterdam Commission in "Het. Institut," No. 2, 1843; "Gazette Médicale," Mars 16, 1844; Voit's Paper in the "Zeitschrift für Biologie," Band viii. 1872, p. 297; and Etzinger idem, Band x. p. 84.

That Gelatin is not destitute of nutritive value is shown by the fact that in one of Bischoff and Voit's experiments a dog, weighing about 80 lbs., lost in four days one pound in body weight when fed with 500 grammes (1 lb. 1 oz. avoird.) of meat alone, but gained in three days 134 grammes (2069 grains) when the same quantity of meat was given together with 200 grammes (3088 grains) of gelatin. That gelatin, even when given in considerable quantities, will not support life, is shown by the results of another experiment, in which a dog weighing over 50 lbs. died on the 31st day when supplied with 3088 grains of gelatin, 2316 grains of starch, 1544 grains of fat, and 185 grains of flesh extract. Etzinger has shown ("Zeits. f. Biologie," B. x.) that ligament, cartilage, and bone, are all largely soluble, with loss of their gelatinifying power, in gastric juice, and are all capable of absorption. Liebig's essence of meat contains from 16—21 per cent. of water, 18—22 per cent. of ash, and 56—60 per cent. of substances soluble in alcohol of 80 per cent. strength and no gelatin or fat. (Thudichum, "On the Origin, Nature, and Uses of Liebig's Extract of Meat," Pamphlet, 1869). In regard to the physiological action of beef-tea and the extract of meat, the reader may refer to the pamphlets on this subject by Kemmerich, Beljawsky, Bogoslowsky ("Centralblatt, f. d. Med. Wiss." No. 32, 1871, and "Archiv f. Anat. u. Phys." 1872); and to Bunge ("Centralblatt," 1871, p. 636). Kemmerich attributed their good effects exclusively to the influence of the alkaline salts they contain, a view that is not supported by the results of experiments performed by other observers.

whole day in the saddle, and lead a life of constant activity resembling that of a carnivorous animal, scarcely ever taste anything but beef; and of this their consumption is by no means great; for the temperature of the surrounding atmosphere is so high that the body has no occasion to generate more heat than is supplied by the combustion of the hydrocarbonaceous portion of the albumen of the food or of "waste" of the tissues. Here, then, the demand for histogenetic material being at its maximum, and that for combustive materials at its minimum, the former supplies all that is requisite for the latter. Again, the Esquimaux and other dwellers upon the Arctic seas find in the bodies of the whales, seals, &c., whereon they subsist, that special supply of the very best combustive material, which alone can enable them to maintain their existence in a climate where the thermometer is for many weeks or months in the year at $-40°$ or even lower, and where the amount of heat which must be generated within the body is four or five times that for which a diet of bread will suffice.—On the other hand, the general experience of the inhabitants of warm climates seems in favour of a diet chiefly or entirely *vegetable;* and its peculiar suitableness appears to consist in its affording an adequate supply of the plastic alimentary substances, in combination with farinaceous matters that give the requisite *bulk* to the food, without affording more combustive material than the system requires,—the quantity of starch which undergoes conversion, and which is introduced as sugar into the circulation, being apparently governed rather by the demands of the respiratory process than by the amount ingested; and the remainder being voided again unchanged.

66. In a well-arranged system of diet the proportion that the non-azotized substances ought to bear to the azotized should be determined by the proportion of Carbon and Nitrogen which are eliminated in the excreta of a healthy man in a given period. Now we know from various experiments that with active exertion about 300 grains of Nitrogen and 4600 grains of Carbon are daily discharged by the several channels of the lungs, skin, kidneys, and bowels; the proportion of the Nitrogen to the Carbon eliminated being, therefore, nearly as 1 : 15. Now, if we compare the composition of bread and of meat, we shall see what is their relative value as aliments, by the proportion which the C holds to the N. According to Payen,* 1000 grains of Bread contain, in round numbers, 300 of Carbon, and 10 of Nitrogen; hence, to obtain the 300 grains of Nitrogen required by the system, 30,000 grains (or more than 4 lbs.) of Bread must be consumed; but the 4600 grains of Carbon required are contained in 15,000 grains of Bread; so that to obtain the requisite supply of Nitrogen a quantity of Bread must be consumed containing exactly double the quantity of Carbon required. Hence it is advantageous to add to a Bread diet a small quantity of Cheese or other highly nitrogenous food. Again, in the case of Meat, 1000 grains contain 100 of Carbon and 30 of Nitrogen; therefore, to obtain the 4600 grains of Carbon, no less than $6\frac{1}{2}$ lbs. must be consumed, whilst the requisite 300 grains of Nitrogen are contained in $1\frac{1}{2}$ lb. of Meat; consequently three or four times more meat must be consumed to supply the Carbon than is necessary to furnish the Nitrogen. The following Table will show how an admixture of bread and meat would require a much less consumption of both than if each were taken separately:—

		Grains of Carbon	*Grains of Nitrogen.*
15,440 grains of	Bread contain	4,630	154
4,630 „	Meat contain	463	154
		5,093	308

* "Des Substances Alimentaires," Paris, 1854.

Thus about 2 lbs. of bread and ¾ lb. of meat are amply sufficient to compensate the daily losses of the system of a healthy man.* Hence we see the immense advantage as to economy of food which a fixed agricultural population possesses over those wandering tribes of hunters which still people a large part both of the Old and New Continents. The *mixed* diet, to which the inclination of man in temperate climates seems usually to lead him (when circumstances allow that inclination to develop itself freely), appears, moreover, to be fully conformable to the construction of his dental and digestive apparatus, as well as to his instinctive propensities. And whilst on the one hand it may be freely conceded to the advocates of "Vegetarianism" that a well-selected vegetable diet is capable of producing (in the greater number of individuals) the highest *physical* development of which they are capable, it may on the other hand be affirmed with equal certainty that the substitution of a moderate proportion of animal flesh is in no way injurious, whilst, so far as our evidence at present extends, this seems rather to favour the highest *mental* development.

67. It is exceedingly difficult to give even an approximation to the composition of the ordinary butchers' meat used as food, since the analyses of different chemists vary considerably; some selecting the muscles alone and the heart, others taking the whole body. The average constitution of entire carcasses of butchers' meat, as given by Messrs. Lawes and Gilbert, the fat being included, is in 1000 parts:—

Animals as fattened for the butcher.	Water.	Dry nitrogenous substance.	Fat.	Mineral matter.
Calf	625	165	166	45
Bullock	500	160	300	50
Lamb	505	110	350	35
Sheep	440	125	400	35
Pig	385	100	500	15

Moleschott gives the following as the composition of the principal animal foods:—

In 1000 parts.	Flesh of Mammals.	Flesh of Birds.	Fish.	Liver.	Eggs.	Milk.
Water	728·75	729·83	740·82	720·06	735·04	861·53
Albuminous compounds	174·22	202·61	137·40	128·20	194·34	39·43
Collagen	31·59	14·00	43·88	37·33	—	—
Fat	37·15	19·46	45·97	35·04	116·37	49·89
Carbohydrates	—	—	—	—	—	43·23
Extractives	16·90	21·11	16·97	65·26	3·74	—
Salts	11·39	12·99	14·96	14·06	10·51	5·92

And the following as representing the composition of the principal Vegetable foods:—

In 1000 parts.	Corn flour.	Legumes (dried peas).	Potatoes.	Beetroot.
Water	150·00	—	760	822·50
Albuminous compounds	132·50	280	10	20·40
Starch	606·80	573	180	—
Sugar, Dextrin	54·80	—	—	122·60
Cellulose	26·60	76	40	25·60
Fat	16·80	—	—	—
Salts	12·50	38	10	8·90

* See Béclard, "Traité Elémentaire de Physiologie," p. 570 *et seq.* 1862. G. Meyer ("Zeits. f. Biol." Band vii. Heft 1) has made a series of interesting observations on the effects of exclusive bread diet on man and dogs. White bread furnished a smaller amount of

According to Dr. Lankester,* 21 oz. of wheat are required to make 1 lb. of flour; and in 1 lb. of flour there are contained—of water $2\frac{1}{4}$ oz., gluten 2 oz., albumen $\frac{1}{4}$ oz., starch $9\frac{1}{2}$ oz., sugar 1 oz., gum $\frac{1}{4}$ oz., fat $\frac{1}{8}$ oz., fibre $\frac{1}{4}$ oz., ashes $\frac{1}{4}$ oz. The carbon contained in 1 lb. of flour amounts to 7 oz. Oysters, which are very digestible and highly nutritious, contain 80·4 parts of water, 14 parts of nitrogenous compounds, 1·5 part of fat, salts 2·7, non-nitrogenous compounds and loss 1·4. According to M. Chevreul, the composition of good beef-tea per litre (1·76 English pint) is:—

Water	985·600
Solid organic substances, dried in vacuo at 68° F.	16·917
Salts	11·263

68. When the results of Experience, then, are combined with the teachings of Science, they seem to justify the following conclusions:—

I. That a due adjustment of the Albuminous, Oleaginous, Saccharine, and Saline constituents of the food, to the varying conditions under which Man exists, is of the first importance; whilst the question of the derivation of the first two of these constituents from the Animal or from the Vegetable kingdom, is one of secondary character; each being capable of yielding them in adequate amount, and the only condition being, that the articles of food shall be so selected as to supply the needful quantity. At the same time it will obviously be requisite that differences should be made in the diet, in accordance with climatic and seasonal variations. For when the external temperature is low an ample supply of oleaginous matter is indicated, and may be advantageously taken in the form of butter, cocoa, fat meat, or maize-bread. On the other hand, during the heat of summer, the more nearly the diet is assimilated to that of the natives of tropical climates, in the substitution of fruits and farinacea for oleaginous articles, the less will be the liability to disordered health in the autumn.†

II. Experience teaches, however, that it is not a matter of entire indifference whether the Albuminous constituent be drawn from the Animal or from the Vegetable kingdom; for the use of a highly animalized diet has a tendency to *raise*, and that of a vegetable diet to *lower*, the proportion of red corpuscles in the Blood; whilst, by a due adjustment of the proportion of the two classes of components, the evil effects of the exclusive use of either may be prevented.

III. So, again, Experience teaches what could scarcely have been anticipated theoretically:—namely, that, notwithstanding the power which the living body possesses of converting saccharine compounds into oleaginous, the

fæces, containing also less nitrogen than Munich rye bread, North German black bread, or the Horsford Liebig's bread, but the feeling of hunger after four days was much greater than with the other kinds of bread. It was found impossible to give sufficient bread to maintain the individual at his full weight, though no less than 94·4 per cent. of the dry material was absorbed. See also Dr. Pavy on the "Physiology and Therapeutics of Food." *Lancet*, 1871–72; and his "Treatise on Food." 1875.

* "Guide to the Food Collection in the South Kensington Museum," p. 39.

† There can be no doubt that a large proportion of the diseases of the digestive apparatus, which are so fatal among European residents in India and other tropical climates, result from the habitual ingestion of a much larger quantity of food, and this especially of a rich and stimulating character, than the system requires. The loss of appetite consequent upon the diminution of the demand for combustive material is set down to the deleterious influence of the climate; and an attempt is made to neutralize this by artificial provocatives.—So, it seems probable that many of the "bilious attacks" which, in this country, are so frequent in early autumn, and which are commonly set down to the account of fruit (although the subjects of them have often abstained entirely from that article), are really the result of the presence of an excess of hydrocarbonaceous matter in the system, consequent upon over-feeding during the summer, and must be looked upon as the natural means by which it is got rid of.

ingestion of a certain amount of Oleaginous matter *as such* is necessary, or at least is favourable, to the maintenance of health. We see this provided in large quantity, in the first aliment prepared by Nature for the offspring of the Mammalia; in the yolk of the egg of all Oviparous animals; whilst, as the laborious investigations of Messrs. Lawes and Gilbert* have shown, the amount of fat contained in ordinary butchers' meat of good quality, to which such a high per-centage of nitrogen is usually attributed, is exceedingly great, varying from one-third to one-half of its weight. In the ordinary diet of every nation on the globe,—whether this be animal, vegetable, or mixed,—we find one or more articles of an oleaginous nature; and there is a natural craving for such substances when they are completely withheld, which indicates that they serve some important purpose in the economy. Although this craving is so far affected by climate that it leads to the largest consumption of oily matter where the extreme of cold has to be endured, it exists with no less intensity even in tropical regions; and we find the Hindoo adding his modicum of "ghee" (or rancid butter made from bisons' milk) to the rice which constitutes his staple article of diet, with the same relish that the Esquimaux feels for his massive lumps of blubber.—It does not seem difficult to understand the *rationale* of this fact. For whilst the Adipose and Nervous tissues are the only portions of the Animal fabric into which fatty matter enters in any considerable proportion, yet its presence has an important influence on the assimilation of albuminous matters, and seems essential to every act of tissue formation. There is strong and increasing reason to believe that a deficiency of oleaginous matter, in a state fit for appropriation by the nutritive processes, is a fertile source of diseased action, especially of that of a tuberculous character: and that the habitual use of it in a larger proportion would operate favourably in the prevention of such maladies, as the employment of cod-liver oil unquestionably does in their cure. A most remarkable example of this is presented by the population of Iceland; which, notwithstanding the concurrence of every one of the circumstances usually considered favourable to the scrofulous diathesis, enjoys a most remarkable immunity from it,—without any other assignable cause than the peculiarly oleaginous character of the diet usually employed.

IV. Another of the results of Experience, of which Science has not yet given a definite *rationale*, is the necessity of employing *fresh vegetables* as an article of Diet; the almost invariable consequence of the entire omission of them being the development of that peculiar constitutional disorder which is known as *Scurvy*.† That the deficiency of something which fresh vegetables can alone supply is the essential cause of this disease (its operation being promoted, however, by other conditions, such as absolute deficiency of food, confinement, bad ventilation, depression of spirits, &c.), may now be regarded as a well-established fact; and it is one which ought to have an important influence on our dietetic arrangements. For if the total withdrawal of these articles be productive of such a fearful depravation of the blood as perverts every function to which the blood is subservient, a diminution of them below the standard requisite for the maintenance of health must necessarily involve a depravation similar in kind though less aggravated in degree; and this, if slight, may be expected to manifest itself, not so much in the production of idiopathic disorders, as in favouring any peculiar tendency to disease which may exist in

* "Phil. Trans." 1859, Pt. ii. p. 495.

† For a full inquiry into this subject, see the "Brit. and For. Med.-Chir. Rev." vol. ii. p. 439.

the system, and in preventing or retarding recovery.* The employment of fresh fruits and of green vegetables seems especially indicated, where a general chronic disorder of nutrition indicates a perverted condition of the circulating material; and especially where there is a disposition to chronic inflammation, induration, and ulceration, in different parts of the body.

v. Finally, then, a well-arranged dietetic scheme ought to consist of such a combination of the Albuminous, Oleaginous, and Farinaceous constituents, as is most appropriate to the requirements of the system;—a larger measure of both the *albuminous* and *farinaceous* or *oily* being supplied, when an unusual amount of nervo-muscular exertion is put forth, and this supply being in the latter case most advantageously derived from animal flesh;—a larger measure of the *oleaginous* being required for the sustentation of the heat in a frigid atmosphere, and this being supplied equally well by the Vegetable kingdom as by the Animal;—and a larger proportion of the *farinaceous*, as a substitute for the oleaginous, being most favourable to health under a high atmospheric temperature. An habitual excess in the use of either of these constituents, above what the demands of the system require, tends towards the production of a particular "diathesis" or constitutional state, which may manifest itself in a great variety of modes. Thus, an excess of the *albuminous* components, such as is only likely to occur when too large a proportion of animal food is employed, undoubtedly favours the *arthritic* diathesis, which seems to consist in the presence of imperfectly-assimilated histogenetic substances and wrongly-metamorphosed products of disintegration, that are not duly eliminated through the kidneys; and this diathesis not only displays itself in gout and gravel, but modifies the course of other diseases. So, again, an excess of the *oleaginous* constituents of the food tends to the production of the *bilious* diathesis, in which, through the insufficient elimination of hydrocarbonaceous matters, the blood becomes charged with the elements of bile. The excess of *farinaceous* matters, moreover, especially when combined with a deficiency of the albuminous (as it too frequently is among those who are obliged by necessity to live chiefly upon a "poor" vegetable diet), tends to the production of the *rheumatic* diathesis; which seems to consist, like the arthritic, in the mal-assimilation and wrong metamorphosis of the components of the tissues, but to be especially favoured by the presence either of lactic acid, or of some other product of the metamorphosis of the saccharine compounds. And, as already pointed out, the deficiency of oleaginous matters seems to tend to the development of the *scrofulous* diathesis; and that of fruits and fresh vegetables to the production of the *scorbutic*.†

* This "scorbutic tendency" was fully recognised by the past generation of Physicians, who practised in those good old times when potatoes were a luxury and green vegetables in the winter almost unknown, when the middle classes fed upon salted meat during a great part of the year, and when sagacious old women prescribed nettle-tea and scurvy-grass, with a course of lenitive "spring-physic," for the "cleansing of the blood."

† It is worthy of remark that in the times when even the wealthy lived during four or five months of the year almost exclusively upon meat, bread, and flour-puddings, and when, therefore, the diet was far too highly-azotized, as well as deficient in fresh vegetables, Arthritic, Calculous, and Scorbutic disorders were much more common than at present. The introduction and universal employment of the potato has unquestionably done much to correct these two tendencies; on the one hand, by diluting the azotized constituents of the food, so that, with the same bulk, a much smaller proportion of these is now introduced; and on the other, by supplying to the blood some element which is essential to the maintenance of its healthy condition. But with the diminution of the Arthritic diathesis, which the experience of our older practitioners, and the medical writings of the last century, indicate as having taken place during that period, there has been an increase in the Rheumatic;—a change which seems to have a close relation to this alteration in diet. And it seems not improbable, too, that this alteration has also much to do with that diminished power of sustaining active

69. The *absolute quantity* of Food required for the maintenance of the Human body in health varies so much with the age, sex, constitution, and habits of the individual, and with the circumstances in which he may be placed, that it would be absurd to attempt to fix any standard which should apply to every particular case. The appetite is the only sure guide for the supply of the wants of each; but its indications must not be misinterpreted. To eat *when* we are hungry is an evidently natural disposition; but to eat *as long as* we are hungry may not always be prudent. Since the feeling of hunger does not depend so much upon the state of fulness or emptiness of the stomach, as upon the condition of the general system, it appears evident that the ingestion of food cannot *at once* produce the effect of dissipating it, though it will do so after a short time; so that, if we eat with undue rapidity, we may continue swallowing food long after we have taken as much as will really be required for the wants of the system; and every superfluous particle is not merely useless, but injurious. Hence, besides its other important ends, the process of thorough mastication is important, as prolonging the meal, and thus giving time to the system to be made acquainted (as it were) that the supply of its wants is in progress; so that its demands may be abated in due time to prevent the ingestion of more than is required. It is very justly remarked by Dr. Beaumont, that the cessation of this demand, rather than the positive sense of satiety, is the proper guide. "There appears to be a sense of perfect intelligence conveyed to the encephalic centre, which, in health, invariably dictates what quantity of aliment (responding to the sense of hunger and its due satisfaction) is naturally required for the purposes of life; and which, if noticed and properly attended to, would prove the most salutary monitor of health, and effectual preventive of disease. It is not the sense of satiety, for this is beyond the point of healthful indulgence, and is Nature's earliest indication of an abuse and overburden of her powers to replenish the system. It occurs immediately previous to this; and may be known by the pleasurable sensations of perfect satisfaction, ease, and quiescence of body and mind. It is when the stomach says, *enough;* and it is distinguished from satiety by the difference of sensations,—the latter saying *too much*." Every medical man is well aware how generally this rule is transgressed; some persons making a regular practice of eating to repletion; and others paying far too little attention to the preliminary operations, and thus ingesting more than is good for them, even though they may actually leave off with an appetite.

70. Although no universal law can be laid down for individuals, it is a matter of much practical importance to be able to form a correct *average* estimate. But even this is given somewhat differently by different observers. Dr. Dalton, for instance,* states that the entire quantity of food required every 24 hours by a man in full health and taking free exercise is, of meat 16 oz. av., bread 19 oz., fat $3\frac{1}{2}$ oz., and of water 52 fl. oz.—that is, about $2\frac{1}{2}$ lbs. of solid food, and rather more than 3 pints of fluid. Vierordt† considers the adult to be well nourished if, with moderate exercise, he receives daily about 4 oz. of

depletory treatment, which, according to the observations of practitioners of long experience characterizes the present generation as compared with the preceding. But whilst there is a diminished capability of bearing large blood-lettings, violent purgation, &c., there is at the same time such an increased tendency to a favourable termination in many of those diseases for which they were formerly accounted necessary, as should remove all regret at this change of constitution.—On the question of "Vegetarianism," the author may refer to his articles on that subject in the "Brit. and For. Med.-Chir. Rev." vol. vi. pp. 76 and 399.

* "Physiology," 1861, p. 97.

† "Grundriss d. Phys.," 1860, p. 192. See also J. Förster, "Zeitsch, f. Biologie," Band ix. 1873, p. 381.

dry albumen, 3 oz. of fat, 11½ oz. of some starchy substance, and about 1 oz. of salts, which gives a proportion of one part of nitrogenous to three and a half parts of non-nitrogenous food. If to this about 6 pints of water, and the oxygen taken up in the act of respiration, which he estimates at 1½ lb., be added, we shall obtain a total of about 1-20th of the weight of the body as the quantity to be ingested in 24 hours. It is from the experience afforded by the usual consumption of food by large bodies of men that our best data are obtained; and these data are sufficient to enable us to predict with tolerable accuracy what will be required by similar aggregations, though they can afford no guide to the consumption of individuals. Parkes and De Chaumont,* who chiefly draw their conclusions from observations made on the diet of soldiers, consider that the standard diet for a male European adult of the average height of 5ft. 6in. to 5ft. 10in., and average weight of 140 to 160 lbs., performing moderate work, may be taken to be 4·5 oz. of dry albuminous substances, 3 oz. of fat, 14 oz. of carbohydrates, and 1 oz. of salts, or 23 oz. of water-free food daily. So that each 1 lb. of body weight receives 0·15 oz., or the whole body receives nearly 1-100th of its weight of dry solids per diem. A certain proportion of water is, however, constantly present, amounting to 50 or 60 per cent., and in addition from 50 to 80 oz. of water are taken in the liquid form; so that on an average 0·5 oz. of water is ingested for each 1 lb. of body weight. Where greater exertion, either mental or bodily, is made, the food must be correspondingly increased in quantity. Thus the average daily water-free diet required for an adult man in very laborious work is—of albuminates, 6 to 7 oz., fats, 3·5 to 4·5 oz., carbohydrates, 16 to 18 oz., salts, 1·2 to 1·5 oz., with a large addition to the quantity of water to compensate for the increased loss by evaporation from the skin and lungs. Great variations of course occur consequent on differences of size and weight as well as upon activity of the organic functions.

The information collected by Dr. Edward Smith for the Government,† showed, indeed, that some people eat ten times more food, in point of nutriment, than others, and that in whole classes of the community a difference of one-half in the amount obtained by the lowest fed is common. From the extended experiments he made on the amount of Carbon daily eliminated by men in good health during the middle period of life when at perfect rest, it appeared that it amounts to 7·9 oz., with the estimated exertion of the middle and light labouring classes to 9·5 oz., and with the estimated exertion of the hard labouring classes to 12·5 ounces. On an examination of the nature of the food actually consumed by these classes, it was found that the proportion of Carbon present was approximately represented by the above numbers; indoor labourers, as cotton and silk operatives, needle-women, and shoemakers, consuming about 10·5 oz., and agricultural labourers in England, 13·2 oz.; in Great Britain and Ireland, 14·1 oz. Hence it may be stated that the adult body requires an average minimum daily amount of Carbon of 9½ to 10½ ounces in the middle and light labouring classes, and of 12½ to 14 ounces in the ordinary hard labouring classes, that is from 25 to 30 grains per lb. weight of the whole body. It is interesting to notice that the infant consumes no less than 136 grains of Carbon for each pound of body weight, a proportion three to four times greater than that actually obtained by the poor in adult life. As regards the amount of Nitrogen, Dr. Smith's observations showed that about 200 grains of Nitrogen are used up daily in the working of the body by the light labouring classes, whilst in the middle and well-fed

* Parkes, "Practical Hygiene," 5th edit., edited by De Chaumont, 1878, p. 192. See also Pavey, "Treatise on Food," 1875, p. 458. † See "Practical Dietary," 1864, p. 20.

classes the total evacuation by all the excretions was 260 grains. The actual amount obtained in food by the indoor classes was 183 grains, and by the outdoor labourers in England 242 grains; and hence we may place the supply of the adult body daily at 200 grains with light occupation, and 250 grains for ordinarily hard working labourers, or from 1 to 1½ grain per lb. of body weight. This quantity is, however, undoubtedly insufficient for the maintenance of thoroughly sound health; and the proportions already given of 300 grains of nitrogen, and 4000 or 4500 grains of carbon with 460 grains of salts, are those which experience indicates as best fulfilling the requirements of the body in the case of a healthy adult with moderately active exertion. The proportion of nitrogen to carbon in such a diet is as 1:15, or expressing it in another way, if the proportions of nitrogenous substances in a standard diet be taken as 1, the fats should be ·6, the carbohydrates 3, and the salts 1·5. In the infant at the breast the proportion of nitrogen consumed to the body weight is stated by Dr. Smith to be six times as great as in the adult. The salts seem to be made up of chlorine 120 grains, phosphoric acid 50 grains, potash 40, soda 40, lime about 4 grains by the urine and some by the bowels, magnesia 4·7 grains by the urine, and a considerable amount by the bowels and iron, the amount of which is uncertain. The following is a dietary furnished by Dr. Smith,* which he considered may be taken as the substantial part of a proper and moderate quantity of food for a man in good health with a good appetite, and making a moderate degree of exertion:—*Breakfast.*—¾ pint of milk; ¼ pint of water with coffee or tea; bread, 4 oz. to 6 oz.; butter, ¾ oz.; sugar, ¾ oz.; bacon, 3 oz., or eggs, 4 oz., or cooked meat, 3 oz. *Dinner.*—Cooked meat, 4 oz. to 6 oz.; potatoes, 8 oz.; bread, 3 oz. to 4 oz.; pudding, 8 oz.; cheese, ½ oz.; soup, 6 oz.; water or beer, ½ pint. *Tea.*—Water with tea, ¾ pint; sugar, ¾ oz.; milk or cream, 2 oz.; bread, 3 oz.; butter, ½ to ¾ oz. *Supper.*—Milk, ¾ pint; oatmeal, 1 oz., and bread 3 oz. to 4 oz., or eggs, 4 oz., or cooked meat, 3 oz., and bread, 3 oz.; butter or cheese, ½ oz.; water or beer.

In the case of Prisoners, the diet should be, of course, as spare as possible, consistently with health; but it should be carefully modified, in individual cases, according to several collateral circumstances, such as depression of mind, compulsory labour, previous intemperate habits, and especially the length of confinement. It has been supposed by some that prisoners require a fuller diet than persons at large; this is probably erroneous; but some variety is certainly desirable to counteract, as far as possible, the depressing influence of their condition upon the digestive powers. The evil effect of an undue reduction in the supply of food, and of insufficient attention to its quality, has unfortunately been too frequently displayed in our prisons; a notable example of which will be hereafter alluded to (§ 81).

71. The smallest quantity of food upon which life is known to have been supported with vigour during a prolonged period, is that on which Cornaro states himself to have subsisted; this was no more than 12 oz. a day, chiefly of vegetable matter, with 14 oz. of light wine, for a period of 58 years. There is another well-known case (that of Thomas Wood, the miller of Billericay, reported to the College of Physicians in 1767 by Sir George Baker), in which a remarkable degree of vigour was sustained for upwards of eighteen years, upon no other nutriment than 16 oz. of flour (containing about 14 oz. of *dry* solids) made into a pudding with water, no other liquid of any kind being taken. There are probably few, however,—at least among those whose avocations require much mental or bodily exertion,—who could long

* For numerous other dietaries, see Pavy, "A Treatise on Food," 1874.

persevere in such a diet. Still it is certain that life with a moderate amount of vigour may be preserved for some time on a very limited allowance of food; this appears from the records of shipwreck and similar disasters. In regard, however, to those who have been stated to fast for a period of months or even years, taking no nutriment, but maintaining an active condition, it may be safely asserted that they were impostors, probably possessing unusual powers of abstinence which they took means to magnify.

72. Of the quantity which *can* be devoured at one time, this is scarcely the place to speak; since such feats of gluttony only demonstrate the extraordinary capacity which the stomach may be made to attain by continual practice. Many amusing instances are related by Captain Parry in his "Arctic Voyages;" in one case a young Esquimaux, to whom he had given (for the sake of curiosity) his full tether, devoured in four-and-twenty hours no less than 35 lbs. of various kinds of aliment, including tallow candles. A case has more recently been published of a Hindoo who can eat a whole sheep at a time; this probably surpasses any other instance on record. The half-breed *voyageurs* of Canada, according to Sir John Franklin, and the wandering Cossacks of Siberia, as testified by Capt. Cochrane, habitually devour a quantity of animal food which would be soon fatal to any one unused to it. The former are spoken of as very discontented when put on a short allowance of 8 lbs. of meat a day; their usual consumption being from 12 to 20 lbs.—That a much larger quantity of food than that formerly specified may be habitually taken with perfect freedom from injurious consequences, under a particular system of exercise, &c., appears from the experience of those who are *trained* for feats of strength, pugilistic encounters, &c. The ordinary belief that the Athletic constitution cannot be long maintained appears to have no real foundation; nor does it appear that any ultimate injury results from the system being persevered-in for some time. That "trained" men often fall into bad health on the cessation of the plan, is probably owing in part to the intemperance and other bad habits of persons of the class usually subjected to this discipline. The effects of trainers' regimen are hardness and firmness of the muscles, clearness of the skin, capability of bearing continued severe exercise, and a feeling of freedom and lightness (or "corkiness") in the limbs. During the continuance of the system, it is found that the body recovers with wonderful facility from the effects of injuries; wounds heal very rapidly; cutaneous eruptions usually disappear. Clearness and vigour of mind, also, are stated to be results of this plan.* The injurious effects observed in those who suddenly engage in trials of strength and endurance, as in rowing, running, and gymnastics, are probably attributable to their being undertaken by young persons who have undergone an insufficient amount of training, and who exhaust themselves by exerting their whole nervous ener-

* The method of training employed by Jackson (a celebrated trainer of prize-fighters in modern times), as deduced from his answers to questions put to him by John Bell, was to begin on a clear foundation by an emetic and two or three purges. Beef and mutton, the lean of fat meat being preferred, constituted the principal food; veal, lamb, and pork were said to be less digestible ("the last purges some men"). Fish was said to be a "watery kind of diet:" and is employed by jockeys who wish to reduce weight by sweating. Stale bread was the only vegetable food allowed. The quantity of fluid permitted was 3½ pints *per diem;* but fermented liquors were strictly forbidden. Two full meals, with a light supper, were usually taken. The quantity of exercise employed was very considerable, and such as few men of ordinary strength could endure.—This account corresponds very much with that which Hunter gave of the North American Indians, when about to set forth on a long march. Playfair gives the diet of a prize-fighter in training as 9·8 oz. albuminates, 3·1 fats, and 3·27 starch and sugar. There were 690 grains of nitrogen, and 4366 grains of carbon.

gies, or who induce some physical derangement of the vascular or respiratory system, by the violent muscular efforts put forth.*

73. It is not enough for the healthy support of the body that the Food ingested should contain an adequate proportion of alimentary constituents; it is important that these should be in a wholesome or undecomposing state. That meat which is simply putrescent is to be considered as injurious *per se*, when habitually employed, is scarcely a matter of reasonable doubt. It is true that some nations are in the habit of keeping their meat until it is tainted, having a preference for it in that condition, which seems to have grown out of the supposed necessity for thus employing it; a preference which has its parallel among the epicures in our own country, who consider the *haut goût* essential to the perfection of their venison or woodcock. One of the most remarkable examples of this kind among a civilized people is furnished by the inhabitants of the Färoe Islands, who, according to the report of Dr. Panum, who has investigated their Sanitary condition, live during a large part of the year upon meat in a state of incipient decomposition, and introduce *rast*, or half-decayed maggoty flesh, fowl, or fish, as a special relish at the end of a meal.† The result of such a diet is (as might be anticipated) a continual disorder of the digestive organs, manifesting itself especially by diarrhœa, which also complicates the course of other diseases, and even becomes, from its obstinacy and exhausting character, their most serious complication. Moreover, the Färoese are peculiarly liable to suffer severely from epidemics, when these are introduced among them. Hence, notwithstanding that the usual rate of mortality is very low (only 1 in $64\frac{2}{3}$ annually), it is obvious that there is a certain constitutional condition among them which peculiarly favours the reception and propagation of zymotic poisons; and it is quite conformable to the principles elsewhere laid down, to attribute this to the habitual introduction of putrescent matter with the food. It is probable, indeed, that if it were not for the active lives of the Färoese, and their habitual exposure to a low external temperature, the direct effects of their diet would be far more prejudicial than they are; but a large part of these are probably neutralized by that activity of respiration which the habits of life of this hardy people induce, much of the noxious matter being decomposed and eliminated by the combustive process. Hence it may well be conceived that the effects of putrescent food would be much more decidedly manifested amongst individuals dwelling in close, ill-ventilated apartments: and although the same means of comparison do not exist, since there is no part of our town-population habitually subsisting on such a diet as that of the Färoese, yet there is no want of evidence with regard to the injurious effects of even the occasional employment of putrescent food, especially when any zymotic disease is epidemic.

74. That it is Water which constitutes the natural drink of Man, and that no other liquor can supply its place, is apparent from the most cursory glance at its uses in the system; and it is only necessary here to remark, that the purity of the water habitually ingested is a point of extreme importance. A very minute impregnation with lead, for example, is quite sufficient to develop all the symptoms of chronic lead-poisoning, if the use of such water be sufficiently prolonged. In the case of the ex-royal family of France, many

* See Skey's Letter and subsequent discussion in "Times" of October, 1867.

† See Dr. Panum's 'Observations on an Epidemic of Measles in the Färoe Islands,' in the "Bibliothek for Lægr." 1846; of which an analysis is given in the "Brit. and For. Med.-Chir. Rev." vol. vii. p. 419.

of whom suffered in this manner at Claremont,* the amount of lead was only about one grain per gallon; and in a case subsequently published, in which also the symptoms of lead-poisoning were unequivocally developed, the amount was no more than 1-9th of a grain.† So, again, an excess of the saline ingredients which appear to be innocuous in small quantities, may produce a marked disorder of the digestive organs, and (through them) of the system generally.‡ Moreover, as in the case of food, the presence of a very small amount of putrescent matter is quite sufficient to produce the most pernicious results, when that matter is habitually introduced into the system; and these results, on the one hand, manifest themselves in the production of certain disorders which appear distinctly traceable to the direct action of the poison so introduced; whilst, on the other, they become apparent in the extraordinary augmentation of the liability to attacks of such zymotic diseases as may at the time be prevalent.§ The quantity of water daily consumed is from 3 to 5 pounds; and a slight excess, indicative of its formation in the system, is daily eliminated. The ingestion of large quantities has been shown by Mosler‖ to cause a considerable increase in the discharge of urea and salts in the urine, which appears to be the result of an increased metamorphosis of the albuminous constituents of the blood and tissues. The quantity of alcoholic liquids consumed in the United Kingdom is extraordinarily great. A recent writer (Mr. W. Hoyle)¶ states that in 1878 29,358,715 gallons of home spirits; 10,438,637 gallons of foreign spirits; 16,272,295 gallons of wine; 1,117,316,754 gallons of beer; and about 17,500,000 gallons of cider and British wine were consumed. The proportion of Alcohol in beer varies from 1 to 12 per cent.; in the light wines of France and Germany from 8 to 15 per cent., and in the stronger Spanish wines from 15 to 25 per cent. Besides Alcohol, all wines contain certain volatile Ethers, and more or less of the Acetic, Tartaric, and Tannic Acids. Sugar and Extractives are also commonly present. The use of *Alcohol*, in combination with water and with organic and saline compounds, in the various forms of "fermented liquors," deserves particular notice, on account of the numerous fallacies which are in vogue respecting it.—In the *first* place, it may be safely affirmed that Alcohol cannot answer any one of those important purposes for which the use of Water is required in the system; and that, on the other hand, it tends to antagonize many of those purposes, by its power of precipitating most of the organic compounds, whose solution in water is essential to their appropriation by the living body. *Secondly*, the ingestion of alcoholic liquors cannot supply anything which is essential to the due nutrition of the system; since we find not only individuals, but whole nations maintaining the highest vigour and activity, both of body and mind, without ever employing them as an article of diet. *Thirdly*, there is no reason to believe that Alcohol, in any of its forms, can become directly subservient to the nutrition of the tissues; for it may be certainly affirmed that in common with non-azotized substances in general, it is incapable of transformation into albuminous compounds; and there is no sufficient evidence that even Fatty matters can be generated in the body at

* See the account of this case, which presents many features of great interest, in the "Dublin Quarterly Journal of Medical Science," vol. vii. p. 415.

† See Herapath in "Medical Gazette," Sept. 20, 1850, p. 518.

‡ Of this a very instructive case, which occurred at Wolverton, has been published by Mr. Corfe in the "Pharmaceutical Journal," July, 1848.

§ For ample evidence to this effect, see Dr. Pereira's "Treatise on Food and Diet," pp. 89–91; and the "Report of the General Board of Health on the Epidemic Cholera of 1848 and 1859," pp. 59–63, "Appendix A," p. 14, and "Appendix B," pp. 91–95.

‖ "Archiv des Vereins f. gemeins Arbeit.," Band iii. 1857, p. 398.

¶ "Times," March 11th, 1879.

its expense. *Fourthly*, the operation of Alcohol upon the living body is essentially that of a *stimulus;* increasing for a time, like other stimuli, the vital activity of the body, and especially that of the nervo-muscular apparatus, so that a greater effect may often be produced in a given time under its use than can be obtained without it; but being followed by a corresponding depression of power, which is the more prolonged and severe in proportion as the previous excitement has been greater. The experiments of Anstie and Dupré show that when Alcohol is consumed in moderate quantities, as of two ounces in divided doses, in the course of the day, the merest traces only are eliminated by the excretions. There can be little doubt, therefore, that it undergoes oxidization in the system.* M. Dupré has shown that weight for weight Alcohol evolves about four times the amount of heat or actual energy that is evolved by lean beef.† Yet other researches‡ show that Alcohol in tolerably full doses lowers the temperature of the body, although it increases the force and frequency of the pulse; and the experience of Arctic voyagers is *most decided* in regard to the comparatively low value of Alcohol as a heat-producing material. It is certain that Alcohol is not without its value under certain circumstances; and the views expressed by Dr. Hammond,§ that its effects, injurious or salutary, are in a great measure dependent upon the quantity of food consumed with it, are probably true. When the food is ample in quantity and varied in quality, and the digestion good, Alcohol is unnecessary, exciting the circulation, and tending to produce a plethoric condition of the system; but when the diet is insufficient, or the digestion feeble, the effects of Alcohol, when taken in moderate quantities, seem decidedly beneficial, the body not only ceasing to lose, but actually gaining in weight; the Alcohol either taking the place of the food, or retarding the metamorphosis of the tissues. In conditions of exhaustion it often proves of the greatest utility, and there is reason for believing that it can exert an antiseptic power in certain states of blood poisoning, whilst it exerts a powerful influence over the formation of pus in inflamed parts; partly perhaps by restraining the movements of the white corpuscles of the blood, partly by hardening the walls of the vessels and preventing their escape, and partly by its general power of lessening tissue change and cell-genesis. The Physiological objections to the habitual use of Alcoholic liquors rest upon the following grounds:—*First*, they are universally admitted to possess a *poisonous* character, exhibited when they are taken in tolerably large doses by loss of appetite and diminished muscular power and control over the voluntary movements, with partial paralysis of the sympathetic nervous system, leading to dilatation of the

* And this accounts for the fact that some persons who consume large quantities of fermented liquors become very fat; the hydrocarbonaceous matters in the system being prevented from undergoing the combustive process to which they would otherwise be subject. Much of the fatty deposit in intemperate persons has the character of "fatty degeneration;" the tendency to which is very marked in persons of this class.

† MM. Duroy, Lallemand, and Perrin, "Du rôle de l'Alcool et des Anesthétiques dans l'Organisme," 1860, Dr. Marcet, "Chronic Alcoholic Intoxication," 1862, and Dr. E. Smith, "Cyclical Changes," and more recently Dr. Ssubotin, "Zeitschrift fur Biologie," Band vii. 1871, p. 361, thought that a considerable quantity of the alcohol ingested was discharged unchanged; but as Anstie and Dupré have shown in their papers in the *Lancet*, 1865, and *Practitioner*, 1872, 1873—in which references will be found to the principal authors on this interesting subject—this view arose either from erroneous observations and inefficient mode of testing for alcohol, or to very large doses being administered to small animals like the rabbit, in which case no doubt a considerable quantity is eliminated unchanged. See also in relation to this subject Dr. Richardson, "Reports Brit. Assoc." 1864 and 1869; Schulinus, "Archiv. f. Heilk.," 1866; Parkes and Wollowicz, "Proc. Roy. Soc. 1870;" Schmidt, "Centralblatt," 1875, p. 371.

‡ Ringer, *Lancet*, 1866, vol. ii. p. 208. § "Amer. Journ. of Med. Sciences," Oct. 1856.

smaller vessels; whilst death is the speedy result of very large doses through the suspension of nervous power, which their introduction into the circulation in sufficient quantity is certain to induce. *Secondly*, when habitually used in excessive quantities, universal experience shows that Alcoholic liquors tend to produce a morbid condition of the body at large, and especially of the nervous system; this condition being such as a knowledge of its *modus operandi* on the body would lead the Physiologist to predicate. *Thirdly*, the frequent occurrence of more chronic diseases of the same character, among persons advanced in life, who have habitually made use of Alcoholic liquors in "moderate" amount, affords a strong probability that they result from a gradual perversion of the nutritive processes, of which that habit is the cause. This perversion manifests itself peculiarly in the tendency to "fatty degeneration" of the muscular substance of the heart, of the walls of the arteries, of the glandular substance of the kidney and liver, and of many other parts; and thus gives rise to a great variety of forms of disease. *Fourthly*, the special liability of the intemperate to zymotic diseases seems an indication that the *habitual* ingestion of Alcoholic liquors tends to prevent the due elimination of the azotized products of the disintegration of the system, and thus to induce a "fermentible" condition of the blood. *Fifthly*, extended experience has shown that, notwithstanding the temporary augmentation of power which may result from the occasional use of fermented liquors, the capacity for prolonged endurance of mental or bodily labour, and for resisting the extremes of heat and cold, as well as other depressing agencies, is diminished rather than increased by their habitual employment; and the reason of this, so far as cold is concerned, is sufficiently obvious. Under ordinary circumstances of exposure to cold the circulation of blood through the vessels of the surface, owing to the contraction of the cutaneous capillaries, is greatly reduced, and much less heat is lost by conduction and radiation, the skin alone being a very bad conductor.* When, however, considerable quantities of Alcohol are taken, more or less complete paralysis of the vaso-motor nervous system is the result: the vessels of the skin no longer respond to the stimulus of cold, and the blood traversing them loses a large amount of heat; so that whilst in all instances where the quantity of Alcohol consumed exceeds the moderate limits of 1½—2 oz. per diem, there is diminished power of resistance to cold, this is felt much more acutely in extreme cases, and death may even take place from the general reduction of the temperature.† On these grounds, the Author has felt himself fully justified in the conclusion that, for Physiological reasons alone, habitual abstinence from Alcoholic liquors is the best rule that can be laid down for the great majority of healthy individuals; the exceptional cases in which any real benefit can be derived from their use being comparatively few.‡

75. The very extensive employment of Tobacco by men of almost every rank in society in this country, and the large consumption of Tea and Coffee by both sexes throughout the community, render the study of their effects upon the animal economy particularly interesting, though up to the present time exceedingly few observations have been made. The effects of Tobacco are chiefly due to the absorption of the extremely poisonous liquid alkaloid Nicotin,§ which exists in the plant in combination with Citric and Malic acids,

* See Klug, "Zeits. f. Biologie," Band x. 1874, p. 73.

† A very remarkable example of the effects of cold on whisky and non-whisky drinkers is recorded in the *Lancet*, vol. i. 1871, p. 636.

‡ See his "Physiology of Temperance and Total Abstinence;" also the important Treatise on "Alcoholismus Chronicus," by Dr. Huss of Stockholm, of which an abstract is given in the "Brit. and For. Med.-Chir. Rev." vols. vii. and ix.

§ See Heubel, "Exp. Beiträge," "Centralblatt f. d. Med. Wiss." 1872, p. 641.

and from its remarkable volatility, is contained in and inhaled with the smoke of the smouldering leaves. Its chemical composition is represented by the formula $C_{10}H_{14}N_2$. Dr. Hammond's conclusions (Op. cit.) from his experiments upon the use of Tobacco are, that whilst it only slightly affects the excretion of carbonic acid from the lungs, it diminishes the quantity of fæces, urine, aqueous vapour, and of chlorine, but it increases the amount of uric, phosphoric, and sulphuric acids eliminated by the kidneys,—circumstances which seem to indicate that there is an increase in the interstitial changes taking place in the brain and nervous tissue, of which there are other indubitable signs, as wakefulness, trembling, and nervous excitement. The quantity employed in the experiment was two cigars thrice a day.—These results accord with general experience; and there are few who will not coincide with the remarks made by Sir B. Brodie in a letter to the "Times" on this subject, dated Aug. 27th, 1860, in which he observes that when used in limited quantity, and under circumstances of privation, Tobacco may be not only harmless but absolutely beneficial by soothing and tranquillizing the nervous system, allaying hunger and the uneasy feelings produced by mental and bodily exhaustion; but that in too many instances it is only a bad habit, producing a greater or less degree of derangement of the nervous system, and indisposing to both mental and bodily exertion. Tea and Coffee, though derived from different classes of the Vegetable kingdom, appear to contain nearly the same organic constituents, but in different proportions. In making "Tea" and "Coffee," the Theine, Gum, Sugar, and Tannic Acids they contain are chiefly extracted, whilst the Casein, unless a little soda be added to the water, remains undissolved. It is a singular circumstance that the Alkaloid contained in Tea and Coffee, as well as that in Maté, the shrub used for tea in Paraguay, should have the same chemical composition ($C_8H_{10}N_4O_6 + 2$ Aq.). Strong decoctions of both fluids counteract the tendency to sleep, excite the nervous system and heart, and produce contractions and tremors in the muscles.* Tea is a respiratory excitant while coffee depresses this function. Lehmann† and Böcker‡ consider that tea and coffee diminish the excretion of urea, and consequently the disintegration of the albuminous tissues, whilst they effect an increase in the amount of water discharged. Voit,§ however, from observations on a dog, and Squarey‖ from experiments on men, conclude that coffee possesses little or no influence on the general nutrition of the body.

2. *Of Hunger and Thirst;—Starvation.*

76. The want of solid Aliment, arising from the demands of the system for the materials requisite for the growth and maintenance of the body, and for the combustive process, is indicated by the sensation of Hunger; and that of liquid, by Thirst. The former of these sensations is referred to the stomach, and the latter to the fauces; but although certain conditions of these parts may be the immediate cause of the sensations in question, they are really indicative of the requirements of the system at large. For the intensity of the feeling bears no constant relation to the amount of solid or liquid aliment in the stomach; whilst, on the other hand, it does correspond with the excess of demand in the system, over the supply afforded by the blood; and it is

* See M. Leven in Brown-Sequard's "Archives de Physiologie," t. i. p. 179.

† Liebig's "Annalen," Band lxxxvii. p. 205. ‡ "Archiv d. Vereins f. gemeins." 1853.

§ Henle and Meissner's "Bericht," 1860, p. 402. See also H. Aubert, Pflüger's "Archiv f. Physiologie," Band v. 1872, p. 589.

‖ See Dr. Parkes' "Practical Hygiene," 5th edit. p. 309, note.

caused to abate by the introduction of the requisite material into the circulating fluid, even though this be not accomplished in the usual manner by the ingestion of food or drink into the stomach.

77. That the sense of hunger, however, is *immediately* dependent upon some condition of the Stomach seems to follow from the fact, that it may be temporarily alleviated by introducing into the digestive cavity matter which is not alimentary. Of the precise nature of that condition, we have no certain knowledge. It is easy to prove that many of the causes which have been assigned for the sensation, are but little, if at all, concerned in producing it. Thus, mere emptiness of the stomach cannot occasion it; since, if the previous meal have been ample, the food passes from its cavity some time before the uneasy feeling is renewed; and this emptiness may continue (in certain disordered states of the system) for many hours, or even days, without a return of desire for food. Besides, the stomach may be filled with food, and yet Hunger may be intensely felt, if, from disease of the pylorus or any other cause, there be an obstacle to the passage of the aliment into the intestine, and to the completion of the processes of chylification and absorption, so that the system needs that which the digestive apparatus is unable to provide for it. Again, the sense of Hunger cannot be due, as some have supposed, to the action of the gastric fluid upon the coats of the stomach themselves; since this fluid is not poured into the stomach, except when its production is stimulated by the irritation of the secreting follicles. Nor is it conveyed through the pneumogastric nerves, since, as shown by Dr. John Reid,* after section of these nerves animals take food with no less avidity than previously; indeed, the sense of satiety rather than that of Hunger seems to be abolished, the animals often continuing to gorge themselves with food long after the Stomach has been adequately filled.—It may, perhaps, be a more probable supposition that there is a certain condition of the Capillary circulation in the Stomach, which is preparatory to the secretion, and which is excited by the influence of the Sympathetic nerves, that communicate (as it were) the wants of the general system. This condition may be easily imagined to be the proximate cause of the sensation of hunger, by acting on the nervous centres. When food is introduced into the stomach, the act of secretion is directly excited; the capillary vessels are gradually unloaded; and the immediate cause of the impression on the nervous system is withdrawn.† By the conversion of the alimentary matter into materials fit for the nutrition of the system, the remote demand also is satisfied; and thus it is, that the condition of the stomach just referred-to, is permanently relieved by the ingestion of substances that can serve as food. But if the ingested matter be not of a kind capable of solution and assimilation, or the digestive apparatus cannot effect its preparation, the feeling of hunger is only temporarily relieved, and soon returns in greater force than before.—The theory here given seems reconcilable with all that has been said of the conditions of the sense of Hunger; and particularly with what is known of the effect produced upon it by nervous impressions, which have a peculiar influence upon the capillary circulation. It also corresponds exactly with what we know of the influence of the nervous system, and of mental impressions, upon other secretions (CHAP. XVII.).

78. The sense of Hunger, like other sensations, may not be taken cognizance of by the mind, if its attention be strongly directed towards other objects; of this fact, almost every one engaged in active operations, whether mental or

* "Phys. Anat. and Pathol. Researches," pp. 234—239.

† These views seem to be confirmed by the observations of M. Bernard on the condition of the gastric follicles during the intervals of their functional activity.

bodily, is occasionally conscious. The nocturnal student, who takes a light and early evening meal, and, after devoting himself to his pursuits for several hours uninterruptedly, retires to rest with a wearied head and empty stomach, but without the least sensation of hunger, is frequently prevented from sleeping by an indescribable feeling of restlessness and *deficiency;* and the introduction of a small quantity of food into the stomach will almost instantaneously allay this, and procure comfortable rest. Many persons, again, who desire to take active exercise before breakfast, are prevented from doing so by the lassitude and even faintness which it induces,—the bodily exercise increasing the demand for food, whilst it draws-off the attention from the sensation of hunger.

79. The conditions of the sense of Thirst appear to be very analogous to those of hunger. This sense is not referred, however, to the stomach, but to the fauces. It is probably even more immediately connected with the state of the general system, than that of hunger: for the immediate relief afforded by the introduction of liquid into the stomach is fully accounted-for by the instantaneous absorption of the fluid into the veins, which is well known to take place when there is a demand for it. This demand is increased with almost equal rapidity, by an excess in the amount of the fluid excretions; and it may be satisfied, or at least alleviated, without the introduction of water into the stomach, this having been one of the results observed after the use of saline injections into the veins in cases of Asiatic Cholera, as well as after immersion in a warm bath in cases of extreme dysphagia. Thirst may also be produced, however, by the impression made by peculiar kinds of food or drink upon the walls of the alimentary canal; thus salted or highly-spiced meat, fermented liquors when too little diluted, and other similarly irritating agents, excite thirst; the purpose of which is obviously to cause ingestion of fluid by which they may be diluted.

80. The results of an entire deficiency of Food, or of its supply in a measure inadequate for the wants of the system, constitute the phenomena of *Inanition* or *Starvation.* These have been experimentally studied by M. Chossat* on Birds and Mammals; and the information thence gained leads us to a better comprehension of what is (unfortunately) too frequently exhibited in the Human subject.—The following were the general symptoms noted by M. Chossat:—The animals usually remain calm during the first half or two-thirds of the period; but they then become more or less agitated; and this state continues as long as their temperature remains elevated. On the last day of life, however, whilst the temperature rapidly falls, this restlessness ceases, and gives place to a state of stupor. The animal, when set at liberty, sometimes looks round with astonishment, without attempting to fly; and sometimes closes the eyes, as if in a state of sleep. Gradually the extremities become cold, and the limbs so weak as no longer to be able to sustain the animal in a standing posture; it falls over on one side, and remains in any position in which it may be placed, without attempting to move. The respirations become slower and slower; the amount of urea eliminated diminishes, at first suddenly, and then more slowly, indicating reduced disintegration of the albumins of the blood and tissues; the general weakness increases, and the insensibility becomes more profound; the pupil dilates; and life becomes extinct, sometimes in a calm and tranquil manner, sometimes after convulsive actions producing opisthotonic rigidity of the body. After the first day, in which the fæces contain the residue of the food previously taken, their amount is very small; and they seem to

* "Recherches Expérimentales sur l'Inanition," Paris, 1843. See also Panum, Virchow's "Archiv," Band xxix. p. 241; and Voit, "Zeitschrift f. Biologie," Band ii. p. 307.

consist principally of grass-green biliary matter. Towards the close of life they contain a much larger quantity of water, even when none has been ingested by the animal; and include much saline matter in addition to the biliary.—The average loss of weight in the warm-blooded animals experimented-on by M. Chossat, between the commencement of the period of Inanition and its termination by death, was 40 per cent.; but he met with a considerable variation in the extremes, which seemed to depend chiefly on the amount of fat previously accumulated in the body; those animals losing most weight in which the fat had been most abundant, which were also those that lived the longest.* Taking 40 per cent. as the mean, M. Chossat obtained the following curious results as regards the relative diminution of the several tissues and organs of the body; those which lost *more* than the mean being distinguished from those which lost *less*.

Parts which lose *more* than 40 per cent.		Parts which lose *less* than 40 per cent.	
Fat	93·3	Muscular coat of stomach	39·7
Blood	75·0	Pharynx and œsophagus	34·2
Spleen	71·4	Skin	33·3
Pancreas	64·1	Kidneys	31·9
Liver	52·0†	Respiratory apparatus	22·2
Heart	44·8	Osseous system	16·7
Intestines	42·4	Eyes	10·0
Muscles of locomotion	42·3	Nervous system	1·9

The points most worthy of note in the above Table, are the almost complete removal of the *fat*, and the reduction of the *blood* to three-fourths its normal amount, the diminution, as has since been shown by Valentin and Panum, especially affecting the albumen of the serum; whilst the *nervous system* undergoes scarcely any loss. It would seem, in fact, as if the supervention of death was coincident with the consumption of all the disposable combustive material: and that up to that point, the whole remaining energy of nutrition is concentrated upon the nervous system. And it will be shown hereafter that there is adequate ground for considering death by *starvation* as really death by *cold;* since the temperature of the body is maintained with little diminution until the fat is thus consumed, and then rapidly falls, unless it be kept up by heat externally applied.—As might be expected from the comparative rapidity of interstitial change at the earlier periods of life, it was found by Chossat that the diurnal loss was much the most rapid in young animals, and that the duration of their lives when deprived of food was consequently far less than that of adults. He further ascertained that the results of *insufficient* alimentation were in the end the same as those of entire deprivation of food; the total amount of loss being almost exactly identical, but its rate being less, so that a longer time was required to produce it. Neither he nor Scheffer‡ found that much influence was exerted on the duration of life, by permitting or withdrawing the supply of water; the latter experimenter found that in a dog wholly deprived of water the loss in weight of the different organs was nearly the same as in deprivation of solid food, with the exception of the brain, fat

* There is a well-known case of a fat pig, which was buried in its sty for 160 days, under thirty feet of the chalk of Dover cliff, and which was dug out alive at the end of that time, reduced in weight from 160 lbs. to 40 lbs., or no less than 75 per cent. ("Trans. of Linn. Soc.," vol. xi. p. 411). This extraordinary prolongation of life in this case may be attributed to the retention of the *heat* of the body by the non-conducting power of the chalk, and to the retention of its *moisture* by the saturation of the air in its immediate vicinity, and restriction of its movements.

† Bidder and Schmidt found that the liver of a cat lost about two-thirds of its original weight, and Voit arrived at the same conclusion in the case of a dog.

‡ Ludwig, "Physiologie," 1861, vol. ii. p. 683.

and glandular organs, which were not materially diminished. All the tissues became much drier; the skin, tendons, muscles, intestines, and blood, containing from 4–11 per cent. more solid residue than in health. It appears, however, that in Man death supervenes much earlier when liquid as well as solid aliment is withheld; and the indifference observed by Chossat in the case of Birds is probably due to the fact that they ordinarily drink very sparingly, and eliminate very little water in their various secretions. If absolutely dry food be given, most animals after a short time cease to eat. The experiments of Blundell and Panum show that the life of a dog deprived of food cannot be preserved by the frequent transfusion of the blood of other healthy dogs.

81. The most prominent symptoms of Starvation, as they have been noted in the Human subject, are as follows:—In the first place, severe pain in the epigastrium, which is relieved on pressure; this subsides after a day or two, but is succeeded by a feeling of weakness and "sinking" in the same region; and an insatiable thirst supervenes, which, if water be withheld, thenceforth becomes the most distressing symptom. The countenance becomes pale and cadaverous; the eyes acquire a peculiar wild and glistening stare; and general emaciation soon manifests itself. The body then exhales a peculiar fœtor, and the skin is covered with a brownish, dirty-looking, and offensive secretion. The bodily strength rapidly declines; the sufferer totters in walking, his voice becomes weak, and he is incapable of the least exertion. The mental powers exhibit a similar prostration; at first there is usually a state of stupidity, which gradually increases to imbecility, so that it is difficult to induce the sufferer to make any effort for his own benefit; and on this a state of maniacal delirium frequently supervenes. Life terminates either in the mode described in Chossat's observations, or, as occasionally happens, in a convulsive paroxysm.*—On post-mortem examination, the condition of the body is found to be such as the results of Chossat's observations would indicate—namely, extreme general emaciation and disappearance of fat,† diminution in the bulk of the principal viscera, and almost complete bloodlessness, save in the brain, which still receives its usual supply. It is especially worthy of note that the coats of the small intestines are peculiarly thinned, so that they become almost transparent; and that the gall-bladder is almost invariably turgid with bile, the cadaveric exudation of which tinges the surrounding parts And further, the body rapidly passes into decomposition.

82. Now it is peculiarly worthy of note that the deficient supply of new histogenetic materials appears to check the elimination and removal of those which have become effete; for in no other way can we account for that tendency to putrescence, which is so remarkably manifested during life in the fœtid exhalation and in the peculiar secretion from the skin, and which is shown after death in the rapidity with which putrefaction supervenes. Moreover, towards the close of many exhausting diseases, the fatal termination of which is really due to a chronic inanition, it frequently happens that a "colliquative diarrhœa" comes on, which must be considered as a manifestation of the general disintegration that is making progress even during life. Now, referring to the conditions hereafter to be enumerated, as those which favour the operation of zymotic poisons in the body, it is obvious that no state could be more liable to it than this; since we have not merely that general depres-

* See Rostan in "Diction. de Médecine," art. 'Abstinence;' and Dr. Donovan's 'Account of the Irish Famine of 1847' in the "Dublin Medical Press," Feb. 1848; also a paper by Martin, "Med. T. and Gaz." April, 1861.

† In cases of *acute* starvation, as Dr. Fowler has shown in reference to the case of the Welsh fasting girl (*Lancet*, vol. ii. 1870, p. 150), a considerable amount of fat may be present in the body, and emaciation may not be marked.

sion of the vital powers, which is a predisposing cause of almost any kind of malady, and pre-eminently so of zymotic diseases, but also the presence of a large amount of disintegrating matter in the blood and general system, which forms the most favourable nidus possible for the reception and multiplication of such poisons. And thus it happens that pestilential diseases must certainly follow in the wake of a famine, and carry off a far greater number than perish from actual starvation.

83. Another class of phenomena, however, results from such a deficiency of alimentation as is not adequate to produce the results just described; provided this deficiency be prolonged for a considerable length of time, and especially if it be conjoined with other unfavourable conditions. Of this, a remarkable example was presented at the Millbank Penitentiary in 1823. The prisoners confined in this establishment, who had previously received an allowance of from 31 to 33 oz. of dry nutriment daily, had this allowance suddenly reduced to 21 oz., animal food being almost entirely excluded from the diet scale. They were at the same time subjected to a low grade of temperature, and to considerable exertion; and were confined within the walls of a prison situated in the midst of a marsh which is below the level of the adjoining river. The prison had been previously considered healthy; but in the course of a few months, the health of a large proportion of the inmates began to give way. The first symptoms were loss of colour, and diminution of flesh and strength; subsequently diarrhœa, dysentery, and scurvy; and lastly adynamic fevers, or headache, vertigo, convulsions, maniacal delirium, apoplexy, &c. The smallest loss of blood produced syncope, which was frequently fatal; and after death, ulceration of the mucous lining of the alimentary canal was very commonly found. Out of 860 prisoners, no fewer than 437, or 52 per cent., were thus affected. The influence of concurrent conditions, especially of previous confinement, was here remarkably shown; for those were found to be most liable to disease who had been in prison the longest. That the reduction of the allowance of food, however, was the main source of the epidemic, was proved by the two following facts:—The prisoners employed in the kitchen, who had 8 oz. of bread additional per day, were not attacked, except three who had only been there a few days; and after the epidemic had spread to a great extent, it was found that the addition of 8 oz. to the daily allowance of vegetable food, and $\frac{1}{2}$ oz. to the animal, greatly facilitated the operation of the remedies which were used for the restoration of health.* Very similar observations to these were made by Dr. Jones† on the prisoners confined in Camp Sumpter, one of the Southern prisons, during the late American civil war.‡

* See Dr. Latham "On the Diseases in the Millbank Penitentiary, 1824." A similar example of the effects of prolonged insufficiency of diet was furnished at the Maison Centrale of Nimes, for a highly instructive account of which by M. Boileau-Castelnau, chief physician to the 'Maison Centrale,' see "Ann. d'Hygiène Publ." Janv. 1849.

† See Dr. Austin Flint's "Physiology of Man," vol. ii. p. 39, 1867.

‡ The prisoners numbered upwards of 30,000, and were confined in a space of 27 acres, with little or no shelter from the intense heat of a Southern sun, or from the rain and dew, with festering masses of filth at the very doors of their rude dens and huts, and with the greater portion of the banks of the stream flowing through the stockade, a filthy quagmire of human excrements alive with maggots. The diet consisted of only $\frac{1}{3}$ lb. bacon and $1\frac{1}{4}$ lb. of meal, and even this was sometimes reduced. As a consequence of exposure to these conditions, in less than seven months 10,000 Federal prisoners died, the chief causes of this frightful mortality being diarrhœa, dysentery, scurvy, and hospital gangrene, the last often supervening on the slightest scratch of the surface, or even on the bites of small insects. It is curious to notice that contagious fevers were rare, and typhus unknown. Dr. Jones remarks, in full confirmation of Chossat's experiments on birds, that whilst large numbers of the Federal prisoners were utterly disgusted with the Indian corn supplied to them, in which, for the most part, the husk was not separated from the meal, yet that an urgent feeling of

The diminished power of resisting deleterious influences produced by insufficient aliment was well shown on a large scale by the statistics collected by Dr. Chenu, of the relative mortality of the French and English contingents in the Crimean war. During the first winter (1855) the English army lost 5·79 per cent. of its effective force, whilst the French only lost 2·31 per cent. Great changes were immediately introduced into the diet and general regimen of the English army, with the result that in the following winter, only 441 soldiers succumbed to disease, out of an effective of 50,000, whilst the French troops, badly fed and badly clothed, had no less than 106,000 sick, of whom 20,000 died, out of a total force of 130,000 men. The effects of insufficient alimentation were also exhibited on a large scale during the siege of Paris. The mortality among the feebler members of the community—old people and children—being very great. Besides the soldiers killed in action, upwards of 42,000 persons died in the course of the five months of siege, in excess of the number dying in the corresponding period of the preceding year.* The proportion steadily rose week by week as the supply of food decreased with only one or two exceptions, from the number 1272, who died in the week ending 24th September, 1870, to the number of 4671, who died in the week ending the 3rd February, 1871, the numbers in the three subsequent weeks being rather less.†

84. It is a curious effect of insufficient nutriment, as shown by the inquiries of Chossat (Op. cit.), that it produces an incapability of digesting even the small amount consumed. He found that when turtle-doves were supplied with limited quantities of corn, but with water at discretion, the whole amount of food taken was scarcely ever actually digested; a part of it being rejected by vomiting, or passing off by diarrhœa, or accumulating in the crop. It seems as if the vital powers were not sufficient to furnish the requisite supply of gastric fluid, when the body began to be enfeebled by insufficient nutrition; or perhaps we might well say, the materials of the gastric fluid are wanting. Hence the loathing of food, which is often manifested by those who have been subjected to the influence of an insufficient diet scale in our prisons and poor-houses, and which has been set down to caprice or obstinacy, and punished accordingly, may be actually a proof of the deficiency of the supply which we might expect to have been voraciously devoured, if really less than the wants of the system require.

85. It is extremely important that the Medical Practitioner should be aware that many of the phenomena above described may be induced by the adoption of a system of too rigid abstinence in the treatment of various diseases; and that they have been frequently confounded with the symptoms of the malady itself, and have led to an entirely erroneous method of treating it. "Many cases," says Dr. Copland,‡ "have occurred to me in practice, where the antiphlogistic regimen, which had been too rigidly pursued, was itself the cause of the very symptoms which it was employed to remove. Of these symptoms, the affection of the head and delirium are the most remarkable, and the most readily mistaken for an actual disease requiring abstinence for its removal." The experience of those, especially, who are largely engaged

hunger was not a prominent symptom, and that even when it existed at first, it soon disappeared, the muscular strength at the same time becoming rapidly diminished, the tissues wasted, and the mental faculties to the last degree lethargic.

* Le Bon, "La Vie," &c., Paris, 1874, p. 71. From 18th Sept. 1869, to 24th Feb. 1870, 21,978 persons died; whilst from 18th Sept. 1870, to 24th Feb. 1871 (period of siege), the number of deaths was 64,154.

† See M. Le Bon, "La Vie," &c , 1874.

‡ "Dictionary of Practical Medicine," vol. i. p. 26.

in consulting practice, must have furnished numerous illustrations of the above statement. Dr. Copland mentions the following:—"A professional man had been seized with fever, for which a too rigid abstinence was enforced, not only during its continuance, but also during convalescence. Delirium had been present at the height of the fever, and recurred when the patient was convalescent. A physician of eminence in maniacal cases was called to him, and recommended that he should be removed to a private asylum. Before this was carried into effect, I was requested to see him. A different treatment and regimen, with a gradual increase of nourishment, were adopted, and he was well in a few days, and within a fortnight returned to his professional avocations."

86. The time during which life can be supported under entire abstinence from food or drink, is usually stated to vary from eight to ten days;* the period may be somewhat prolonged, however, by the occasional use of water, and still more by a very small supply of food; or even, it would seem, by a moist condition of the surrounding atmosphere, which obstructs the exhalation of liquid from the body. Thus, Foderé mentions that some workmen were extricated alive after fourteen days' confinement in a cold damp vault, in which they had been buried under a ruin. Dr. Sloan has given an account† of the case of a healthy man, æt. 65, who was found alive after having been shut up in a coal-mine for twenty-three days, during the first ten of which he was able to procure and swallow a small quantity of foul water; he was in a state of extreme exhaustion, and died three days afterwards, notwithstanding the attempts made to recover him. It would seem as if certain conditions of the nervous system, especially those attended with peculiar emotional excitement, are favourable to the prolongation of life under such circumstances. Thus, in a case recorded by Dr. Willan, of a young gentleman who starved himself under the influence of a religious delusion, life was prolonged for sixty days; during the whole of which time, nothing else was taken than a little orange-juice. In a somewhat similar case which occurred under the Author's notice, in the person of a young French lady, more than fifteen days elapsed between the time that she ceased to eat regularly, and the time of her being compelled to receive nourishment; during this period she took a good deal of exercise, and her strength seemed to suffer but little, although she swallowed solid food only once, and then in small quantity. Again, in certain states of the system commonly known as "hysterical," there is frequently a very remarkable disposition for abstinence, and power of sustaining it. It may be well to remark that, under such circumstances, the continual persuasions of anxious friends are very injurious to the patient, whose return to her usual state will probably take place the earlier, the more completely she is left to herself.

3. *Movements of the Alimentary Canal.*

87. The motions by which Food is conveyed to the *Mouth* and introduced into its cavity, constituting the acts of *Prehension* and *Ingestion*, are ordinarily considered to be *voluntary*, at least in the adult; and it is indubitable that the Will has entire control over them. Nevertheless, they belong to the class

* There seems adequate evidence that a state which may be characterized as one of *Syncope*—the animal functions being entirely suspended, and the organic functions being reduced to an extremely low ebb—may be prolonged for many days, or even weeks, provided the temperature of the body be not too much reduced. This class of facts, however, will be more appropriately considered hereafter (CHAP. XXI.).

† "Medical Gazette," vol. xvii. p. 389. F. The Welsh Miners, *Lancet*, Ap. 28, 1877, were 9 days without food, except a few candles, and recovered.

of "secondarily automatic" movements; and like those of locomotion, may be kept-up when the will is in abeyance, by the suggesting and guiding influence of sensations, thus being performed under the same essential conditions as the purely "consensual" or "sensori-motor" actions.* The necessity of "guiding sensations" for their performance is made evident by one of Sir C. Bell's experiments, the wrong interpretation of whose results originally led him to an erroneous view of the functions of the Fifth pair of nerves. He found that an Ass, in which the infra-orbital branch of this nerve had been divided, made no attempt to pick up oats with its lip, although the animal saw them, bent-down its head with the obvious purpose of ingesting them, and brought its lip into absolute contact with them; hence he concluded that the power of *motion* was destroyed in the lip, when it was in reality only the *guiding sensation* that was deficient, the motor power being supplied by the Facial nerve or Portio dura.

88. The food thus introduced into the mouth is subjected (unless it be already in a state which needs no further reduction) to the process of *Mastication*. This is evidently an operation of great importance, in preparing the substances to be afterwards operated-on for the action of their solvent; and it exactly corresponds with the trituration to which the Chemist would submit any solid matter, that he might present it in the most advantageous form to a digestive menstruum. The complete disintegration of the alimentary matter is, therefore, of great consequence; and, if imperfectly effected, the subsequent processes are liable to derangement. Such derangement we continually meet with; for there is not, perhaps, a more frequent source of Dyspepsia than imperfect mastication, whether resulting from the haste with which food is swallowed, or from the want of the instruments proper for the reducing operation. The mechanical disintegration of the food is manifestly aided by Insalivation; but the admixture of Saliva also exerts, as we shall hereafter see, a very marked influence on the chemical composition of certain of its constituents. The movements of Mastication, still more than those already adverted-to, although under the complete control of the Will, and originally dependent upon it for their excitation, come at last to be of so *habitual* a character, that they continue when the direct influence of the will is withdrawn, the influence of the guiding "sensation," however, being essential to their performance. Every one is conscious that the act of mastication may be performed as well, when the mind is attentively dwelling on some other object, as when directed to *it;* but, in the former case, we are rather apt to go on chewing and rechewing what is already fit to be swallowed, simply because the will does not exert itself to check the action, and to carry the food backwards within the reach of the muscles of deglutition. This conveyance of food backwards to the fauces is a distinctly voluntary act; and it is necessary that it should be guided by the sensation which there results from the contact it induces. If the surface of the pharynx were as destitute of sensation as is the lower part of the œsophagus, we should not know when we had done what was necessary to excite its muscles to operation.—The muscles depressing the lower jaw are the genio-hyoid, the mylohyoid, and the anterior belly of the digastric. The omo-hyoid, sterno-hyoid, and thyro-hyoid muscles, also aid. The upward

* This, the Author thinks, will be conformable to the experience of most of his readers; who will find, if they analyze their own consciousness, that they continue to eat while their whole *attention* is given to some abstract train of thought, or to some external object. But a remarkable case has been placed on record by Mr. Dunn (*Lancet*, Nov. 15 and 29, 1845), which fully confirms the view here advanced; the movements, not merely of the lips and jaws, but those by which food was conveyed to the mouth, having been carried on *automatically*, when once (so to speak) the spring was touched by which they were set in action.

movement is effected by the combined action of the masseter, temporal and internal pterygoid muscles. The forward movement is due to the action of both pterygoids, and the lateral or grinding movement to the external pterygoid of one side. The Tongue is moved downwards and forwards by the hyo-glossus and genio-glossus, upwards and backwards by the stylo-glossus, whilst its changes of form are due in great measure to its intrinsic longitudinal and transverse fibres. The more important muscles concerned in the mastication of food are supplied by the third branch of the Fifth pair, which is well known to be a nerve of mixed endowments; but some, especially those of the cheeks, are also supplied by the Facial nerve; and yet, if the former be paralyzed, the latter cannot stimulate them to the necessary combined actions. Hence we see that the movements are of an associated character, their due performance being dependent on the part of the nervous centres, from which the motor influence originates. If the Fifth pair, on the other hand, be uninjured, whilst the Portio dura is paralyzed, the movements of mastication are performed without difficulty; whilst those connected in any way with the Respiratory function, or with Expression, are paralyzed. If, again, the sensory portion of the Fifth pair be paralyzed, the act of Mastication is very imperfectly performed, even though the motor power be not in the least impaired; for the muscles cannot be made to perform the requisite associated movements without the guidance of sensations; so that the morsel lodges between the teeth and the cheek, or beneath the tongue, and can with difficulty be kept in the appropriate position.

89. When the reduction of the food in the mouth has been sufficiently accomplished, it is carried into the *Pharynx*, and is thence propelled down the œsophagus into the stomach, by a set of associated movements, which, taken together, constitute the act of *Deglutition*.* The *first* stage in the process is purely voluntary, and consists in the carrying back of the food until it has passed the anterior palatine arch; this is effected by the contraction of the mylo-hyoid, and of the longitudinal and transverse muscles of the tongue, which together render the tongue shorter and thicker, pressing it against the roof of the mouth, whilst the stylo-glossi draw it somewhat backward. The *second* stage now commences, during which the entrance of food into the nasal cavities and trachea is most jealously guarded against by certain reflex actions, which have only been clearly recognized since the introduction of the laryngoscope by Czermak. During this stage the tongue is carried still farther backwards, the larynx rises, its orifice being covered by the epiglottis, which is at the same time somewhat depressed, and placed horizontally, so that its upper border touches the posterior wall of the pharynx.† The cushion at the base of the epiglottis becomes applied to the arytenoid cartilages, and the vocal cords, both true and false, are closely approximated; a triple protection against the entrance of the food into the trachea being thus afforded. Coincidently with these movements, the lower border of the velum palati becomes applied to the walls of the pharynx, and the muscles of the posterior palatine arch contract in such a manner, as to cause the sides of the arch to approach each

* These movements were first described in detail by Magendie; but his account requires some modification, through more recent observations. See those of Dzondi, in Prof. Müller's "Elements of Physiology" (translated by Dr. Baly), p. 501; Budge ("Phys.," 1860, p. 157); Bidder ("Neue Beobachtungen," Dorpat, 1838); Czermak "The Laryngoscope," New Syd. Soc. Translation, 1861, vol. xi.; Schuh "On the Laryngoscope," Canstatt, 1858; and Moura Robin's "Journal de l'Anatomie," 1867, p. 157; Chauveau in Brown-Séquard's "Journal de la Physiologie," 1862, p. 211; A. Mosso, "Centralblatt der Med. Wiss.," 1874, p. 263).

† The presence of the epiglottis is not essential. After its ablation cats and dogs can still swallow without difficulty or the entrance of food into the larynx. See Walton in Foster's "Journ. of Physiology," vol. i. 1878, p 303.

other like a pair of curtains, the passage from the fauces into the posterior nares being nearly closed by them; and to the cleft between the approximated sides the uvula is applied like a valve. A sort of inclined plane, directed obliquely downwards and backwards, is thus formed; and the morsel slides along it into the pharynx, which is brought-up to receive it, by the action of the stylo- and palato-pharyngei muscles. Though some of these acts may be performed voluntarily, the combination of the whole is automatic.* The *third* stage of the process, the propulsion of the food down the œsophagus, then commences. This is accomplished, in the upper part, by means of the constrictors of the pharynx; and in the lower, by the muscular coat of the œsophagus itself, which is composed in its upper part of striated muscular tissue alone, in its middle part of exclusively unstriated muscular tissue, and near the cardiac orifice of the stomach of a mixture of striated and unstriated tissue.† When the morsels are small, and are mixed with much fluid, the undulating movements from-above-downwards succeed each other very rapidly, as may be well observed in Horses whilst drinking; large morsels, however, are frequently some time in making their way down. Each portion of food and drink is included in the contractile walls, which are closely applied to it during the whole of its transit. The gurgling sound which is observed when drink is poured down the throat of a person in *articulo mortis*, is due to the want of this contraction. The whole of the third stage is completely involuntary.—In order to ascertain the parts implicated in the deglutition of liquids, Dr. Moura employed the laryngoscope after ink had been swallowed, and found that the parts tinted were the whole internal surface of the mouth, the velum palati, uvula, pillars of the fauces, anterior surfaces of the epiglottis and the pharynx generally, with the posterior surfaces of the cricoid and arytenoid cartilages. On the contrary, the parts that preserved their natural colour were the interior of the larynx to within a very short distance of the free edge of the epiglottis and the anterior portion of the lateral grooves of the fauces. At the point where the œsophagus enters the stomach, the "cardiac orifice" of the latter, there is a sort of sphincter, which is usually closed, but which opens when sufficient pressure is made on it by accumulated food, closing again, when this has passed, so as to retain it in the stomach.‡

90. The purely *automatic* nature of the act of Deglutition is shown by the fact, that no attempt on our part will succeed in performing it really *voluntarily*. In order to excite it, we must apply some stimulus to the fauces. A very small particle of solid matter, or a little fluid (saliva, for instance), or the contact of the back of the tongue itself, will be sufficient; but without either of these, *we cannot swallow at will*. Nor can we restrain the tendency, when it is thus excited by a stimulus; every one knows how irresistible it is, when the fauces are touched in any unusual manner; and it is equally beyond the

* The observations of Schuh (Canstatt, 1858) upon the movements of the soft palate during deglutition seem to show that this part is somewhat more active during the second stage than it was described to be by Dzondi. He had an opportunity of observing them in a woman, the left side of whose face had been removed by an operation. When the patient drank, the soft palate raised itself above the horizontal line, as soon as the glass was approximated to her lips. It remained in this position whilst the fluid was being sucked in; but as soon as swallowing commenced it very suddenly descended, so as to press the fluid into the œsophagus. It then again elevated itself with even greater tension, and again descended. In swallowing solid food the same sudden ascent and descent of the velum upon the deglutition of each morsel was observable. See also Brücke's "Vorlesungen," Band i. 281.

† Gillette, "Journ. de l'Anatomie," 1872, p. 617. See also for the Histology of the Alimentary Canal, Klein and Verson in Stricker's "Manual of Histology," Syd. Soc. Transl. vol. i.

‡ The closure of the sphincter has been disputed by Giannuzzi.

direct control of the will, in the ordinary process of eating,—voluntary as we commonly regard this. Moreover, this action is performed, like that of respiration, when the power of the will is suspended, as in profound sleep, or in apoplexy affecting only the brain; and it does not seem to be at all affected by the entire removal of the brain, in an animal that can sustain the shock of the operation; being readily excitable, on stimulating the fauces, so long as the nervous structure retains its functions. But if the "nervous" circle be destroyed, either by division of the trunks, or by injury of any kind to the portion of the nervous centres connected with them, the action can no longer be performed; and thus we see that, when the effects of apoplexy are extending themselves from the brain to the spinal cord, whilst the respiration becomes stertorous, the power of Deglutition is lost, and then respiration also speedily ceases.

91. The *nerves* specially concerned in this action are connected with a *reflex centre* situated in the lower part of the medulla oblongata, named the accessory olivary body, the mechanism of which is such that under normal conditions the motor impulses liberated affect first the muscular fibres of the upper part of the œsophagus, and then those of the lower. The centre cannot be excited from the œsophagus, the sensibility of which is low, since if a morsel of food be introduced into it from without, it remains stationary at the point where it has been inserted, until a swallowing movement commencing in the pharynx is propagated to it.* On the other hand, the motor impulse once liberated from the centre, spreads itself from above downwards through the whole length of the œsophagus, as is shown by the fact that if a piece of string be attached to a morsel of meat, and this is pulled up after having been allowed to descend half-way down the œsophagus, the wave of contraction is propagated to the stomach. Even the excision of a complete ring of the œsophagus does not arrest this propagation of the peristaltic contraction of the tube.† The *centripetal* or *sensory impressions* are conveyed to the medullary centre along the descending palatine branches of the second division of the Fifth pair distributed upon the fauces, and along the superior laryngeal branches of the pneumogastric distributed upon the pharynx. The *centrifugal* or *motor impulses* traverse the pharyngeal branches of the Pneumogastric, which are probably originally derived from the Spinal accessory; the branches of the Hypoglossal, distributed to the muscles of the tongue, and to the sterno-hyoid, sterno-thyroid, and thyro-hyoid muscles; the motor filaments of the Recurrent laryngeals; some of the branches of the Fifth, supplying the levator muscles of the lower jaw; the branches of the Facial, ramifying upon the levator palati mollis, the digastric and stylo-hyoid muscles, and upon those of the lower part of the face; and probably some of the branches of the Cervical plexus, which unite themselves to the descendens noni. It was further observed by Dr. Reid‡ that the stylo-pharyngeus muscle is usually thrown into contraction when the roots of the Glosso-pharyngeal nerve are irritated; and as this has been also noticed by Mayo, Volkmann, and others, we are probably to consider the Glosso-pharyngeal a motor nerve, in so far as that muscle is concerned.§ Swallowing

* Steiner, "Physiol.," 1878, p. 146, who quotes from Volkmann.

† See Chauveau in Brown-Séquard's "Journ. de l'Anatomie," 1862, p. 211.

‡ See Dr. J. Reid, "Edin. Med. and Surg. Journ." vol. xlix.; and "Physiological, Anatomical, and Pathological Researches," chap. iv.; Vulpian and Solyet, "Revue de Cours Scientifiques," 1866, t. iii. p. 754.

§ Op. cit. pp. 258—260. It seems not improbable that the discrepant results obtained by different experimenters on this point are partly to be explained by differences in the distribution of the nerves in the several species of animals operated on. Thus in the experiments of Prévost and Waller on the *Rabbit* (Brown-Séquard's "Archives de Physiologie,"

movements can be initiated by stimulation of the larynx, or by direct irritation of the superior laryngeal nerve, of the trunk of the vagus in the neck, or of the recurrent laryngeal nerve.

92. In the propulsion of the food through the œsophagus we have a distinct case of *reflex action, without sensation*, occurring as one of the *regular associated movements* in the natural condition of the animal body; and it is very interesting to find this following upon a reflex action *with* sensation (that of the pharynx), and preceding a movement which is but slightly connected with the Spinal Cord (that of the lower part of the alimentary canal). The use of sensation in the former case has been already shown. The muscular fibres of the Œsophagus are *also* excitable, though usually in a less degree, by *direct* stimulation; for it appears that, in some animals (the Dog, for example), section of the pneumogastric does not produce that check to the propulsion of the food which it occasions in the Rabbit; and even in the Rabbit, as Dr. M. Hall has remarked,* the simple contractility of the muscular fibre occasions a distinct peristaltic movement along the tube, after its nerves have been divided; causing it to discharge its contents when cut across. Such a movement, indeed, seems to take place in something of a rhythmical manner (that is, at short and tolerably regular intervals), whilst a meal is being swallowed; but as the stomach becomes full, the intervals are longer, and the wave-like contractions less frequent. The re-opening of the cardiac orifice, on pressure from *within* (which is usually resisted by the sphincter, as in the acts of defæcation, parturition, &c.), is one of the first of that series of reversed actions which constitutes the act of *Vomiting;* and this is accompanied by a reversed peristaltic action of the œsophagus. The independence of these actions, one of another, and their relation to a common cause, is remarkably shown by the fact, that when vomiting takes place as a consequence of the injection of tartar-emetic into the veins, the reversed peristaltic action of the œsophagus is performed even after its separation from the stomach.

93. The food which, thus propelled along the œsophagus, enters the *Stomach* through its cardiac orifice in successive waves, is immediately subjected to a peculiar peristaltic movement, which has for its object to produce the thorough intermixture of the gastric fluid with the alimentary mass, and so to separate the portion which has been sufficiently reduced, from the remainder. The fasciculi composing the muscular wall of the Human stomach have been shown by Dr. J. B. Pettigrew† to be so disposed as to form long spirals or figure-of-eight loops, of which the most external and most internal fibres are nearly longitudinal, whilst those most centrally situated are nearly circular. The contraction of these fibres lessens the diameter of the stomach in every direction; and whilst the cavity is empty, they are uniformly

1870, pp. 185 and 343), it appeared that in this animal the glosso-pharyngeal nerve takes no part in the reflex phenomena of deglutition, the fifth being the principal sensory nerve, and the superior laryngeal branch of the pneumogastric contributing to the reflex movement by its sensory branches distributed to the mucous membrane covering the epiglossus, the arytenoepiglottidean folds, the superior borders of the laryngeal orifice and the cartilages of Santorini. In Chauveau's experiments on the *Horse* ("Journal de la Physiologie," t. v. pp. 190 and 323), direct irritation of the upper roots of the vagus caused contraction chiefly of the inferior constrictor and of the œsophagus; of the middle roots, contraction of the pharynx generally; and of the lower roots, contraction of the upper constrictor and levator; though all acted to some extent upon the whole pharynx and œsophagus. The spinal accessory, glosso-pharyngeal, facial, hypoglossal, and cervical sympathetic nerves, had little or no action on the movements of the pharynx, œsophagus, or stomach in this animal. See also Goltz ('Studien,' &c., in Pflüger's "Archiv," 1872, vi. p. 616), for the movements of the œsophagus in the *Frog*.

* "Third Memoir on the Nervous System," § 201.

† "Proceed. of the Roy. Soc. Lond.," June 20, 1867.

contracted, so as to reduce the organ to its smallest dimensions. When food is introduced the stomach rotates on its long axis, the surface that looks forwards in the fasting state becoming more and more superior; the contraction of the parietes as a whole still continues to such a degree as to make them closely apply themselves to its surface; but the contraction of the individual fasciculi alternates with relaxation in such a manner as to induce a great variety of motions in this organ, sometimes transversely, and at other times longitudinally. "These motions," remarks Dr. Beaumont, who has enjoyed a peculiar opportunity of observing them,* "not only produce a constant disturbance or *churning* of the contents of the stomach, but they compel them at the same time to revolve about the interior from point to point and from one extremity to the other." In addition to these movements, there is a constant agitation of the stomach, produced by the respiratory muscles. The nature of these, and indeed of all peristaltic movements, has been stated by Dr. Brinton† to resemble very closely those produced by the descent of a perforated piston in a closed tube containing fluid, for here there would be peripheral currents passing in the same direction as the piston, and a central current flowing in the opposite direction, through the perforation in the piston. The direction which the particles of food take, as described by Dr. Beaumont, corresponds very fairly with this view. He says:—"The bolus as it enters the cardia, turns to the left, passes the aperture, descends into the splenic extremity, and follows the great curvature towards the pyloric end. It then returns, in the course of the smaller curvature (or as Dr. Brinton supposes, through the axis of the stomach), and makes its appearance again at the aperture in its descent into the great curvature, to perform similar revolutions. These revolutions are completed in from one to three minutes. They are probably induced, in a great measure, by the circular or tranverse muscles of the stomach. They are slower at first, than after chymification has considerably advanced;" at which time also there is an increased impulse towards the pylorus. It is probable that, from the very commencement of chymification, until the organ becomes empty, portions of chyme are continually passing into the duodenum; for the bulk of the alimentary mass progressively diminishes, and this the more rapidly as the process is nearer its completion. The accelerated expulsion appears to be effected by a peculiar action of the transverse muscles; and especially of that portion of them which surrounds the stomach at about four inches from its pyloric extremity. This band is so forcibly contracted at the latter part of the digestive process that it almost separates the two portions of the stomach into a sort of hour-glass form; and Dr. Beaumont states that, when he attempted to introduce a long thermometer-tube into the pyloric portion of the stomach, the bulb was at first gently resisted, then allowed to pass, and then grasped by the muscular parietes beyond, so as to be drawn-in: whence it appears that the contraction has for its object, to resist the passage of solid bodies into the pyloric extremity of the stomach, at this stage of digestion, whilst the matter which has been reduced to the fluid form is pumped-away (as it were) by the action of that portion of the viscus. These peculiar motion continues until the stomach is perfectly empty, and not a particle of

* See the "Case of Alexis St. Martin, with Observations and Experiments by Dr. Beaumont," republished in this country by Dr. Andrew Combe.—This patient had a large fistulous orifice in his stomach, remaining after a wound which had laid-open the cavity; but his general health had been completely restored.

† "Cyclop. Anat. and Phys." vol. v. pp. 313 and 345. See also, supporting Dr. Brinton's views, the observations of Dr. v. Braam Houckgeest (Pflüger's "Archiv," 1872, Band vi. p. 300). In these experiments the belly of the animal was opened whilst the animal was immersed in a solution, containing 6-10ths per cent. of common salt in water, at blood heat.

food or of chyme remains: and when they are nearly brought to a close, the contraction of the pyloric orifice also gives way to an extent sufficient to allow not only the undigested residue of the food, but also large solid bodies that may have been swallowed (such as coins and the like), to pass into the intestinal canal.

94. With regard to the degree in which these movements of the Stomach, whose share in the Digestive operation is so important, are dependent upon the Spinal cord, and are consequently of a "reflex" nature, it is difficult to speak with certainty, owing to the contradictory results obtained by different experimenters. These contradictions, however, seem partly due to a diversity in the nature of the animals experimented-on, and partly to a difference in the stage of the digestive process at which the observations were made. The *nerves* supplying the Stomach are derived from the Pneumogastrics, and from branches of the solar plexus of the Sympathetic, and it seems to be well established by the researches of Reid, Valentin, and others,* that distinct movements commencing at the cardiac orifice, and extending peristaltically towards the pylorus may be excited, when the Stomach is distended with food, by irritating the Pneumogastric. The movements, however, are comparatively feeble when the Stomach is empty. When the Pneumogastrics are divided in the neck, the cardiac orifice of the stomach becomes spasmodically contracted† —a condition which, after lasting for about thirty-six hours, generally passes off. If previously to that period the animal be allowed to eat, the food accumulates in the lower part of the œsophagus, and death results from suffocation. The contraction of the cardiac sphincter appears, therefore, to be induced by other nerves than the Pneumogastric; but there is abundant evidence to show that all the ordinary movements of the stomach are governed by the Pneumogastrics (or, perhaps, as Schiff believes, by the fibres of the Spinal Accessory coursing in the Pneumogastrics), since, if these be divided, complete paralysis of the muscular walls results, whilst lively movements can still be induced by irritation of the lower or distal cut extremity. Irritation of the splanchnic nerves, or of the sympathetic cord, is not followed by any very obvious movements, the former nerves being in fact essentially vaso-motor, and as when stimulated they cause contraction of the blood-vessels, they rather tend to inhibit any movements that may be present, than to incite them if they are absent. It is found that after the section of the Pneumogastrics, if small portions of food be introduced into the stomach, these can be still propelled onwards, which we must consider to be due either, as Ludwig‡ and Schiff§ suppose, to the reflex action of the ganglia of the Sympathetic, which are very numerous in the connective tissue layers of its parietes, or possibly to the contractions of the muscular fibres produced by direct irritation, a view which originally advanced by the Author has been strongly advocated by Engelmann.‖ The moderate excitement of pleasurable emotions is favourable to the operation of digestion; not only by

* See Dr. Reid's "Physiological, Anatomical, and Pathological Researches," chap. v.; Valentin, "De Functionibus Nervorum Cerebralium," &c., chap. xi.; also Longet, "Anat. et Physiol. du Système Nerveux," tom. i. p. 323; and "Physiologie," vol. i. 1868; and Bischoff in Müller's "Archiv," 1843. Pincus, "Exp. de vi Nervi Vagi," Wratislaw, 1856; Harting, "Ueber die Nervi Vagi," Giessen, 1858; Schiff, "Physiologie," 1859, p. 420; and Schweiz, "Monats. f. Prakt. Med.," 1860; Bernard, "Med. Times and Gaz.," 1860, vol. ii. p. 1; Ravitsch, Müller's "Archiv," 1861, p. 779; Henle, "Handb. d. System. Anat. des Menschen," Band ii. 1866; O. Nasse "Beiträge zur Physiologie d. Darmbewegung," 1866.

† Bernard, "Med. Times and Gaz.," 1860, vol. ii. p. 1.

‡ "Physiologie," p. 614. § "Untersuchungen zur Naturlehre," viii. p. 323.

‖ Pflüger's "Archiv," Band iv. 1871, p. 1.

giving firmness and regularity to the action of the heart, and thus promoting the circulation of the blood and the increase of gastric secretion, but also in all probability by imparting energy and regularity to the muscular contractions of the stomach. The movements of the stomach cease during sleep.*

95. Much discussion has taken place upon the question, how far contraction of the parietes of the Stomach itself actually participates in the operation of *Vomiting;* and many experiments have been made to determine the facts of the case. Some, like Magendie, have gone so far as to affirm that the stomach is essentially passive; grounding this inference upon the fact experimentally ascertained, that when the stomach was removed, and a bladder was substituted for it, this was emptied of its contents by the compression of the parietes of the abdomen, when tartar-emetic was injected into the veins.† But this fact by no means disproves the active co-operation of the stomach; and judging from the analogy of the uterus, bladder, and rectum,—whose muscular walls are all actively concerned in the expulsion of their contents, though that expulsion is in great part due to the contraction of the abdominal muscles,—we should be led to concur with the common opinion, of which our own sensations during the act would indicate the correctness. From the careful experiments of Schiff‡ on dogs, as well as from observations made on man in cases where, from injury, the stomach has been exposed,§ it appears that under ordinary circumstances the cardiac aperture is firmly closed; but that when vomiting is about to take place, a full inspiration occurs, which serves, as Dr. M. Hall first pointed out, to fix the diaphragm and to supply a firm surface against which the stomach can be pressed. Then, an instant before the contraction of the abdominal walls occurs, the cardiac orifice is suddenly dilated by the contraction of special bands of muscular fibres, which are probably continuous with the longitudinal fibres of the œsophagus. The muscles of expiration—*i.e.*, the abdominal muscles—then contract with great vigour, and the glottis being closed, so that the escape of air from the chest and the elevation of the diaphragm are prevented, the stomach is subjected to considerable pressure, and its contents are immediately ejected. The importance of the contraction of the abdominal muscles is sufficiently evidenced by the fact, demonstrated by Giannuzzi, that no vomiting can be induced in animals whose voluntary muscles have been paralyzed by curare. When peristaltic movements of the stomach, which have occasionally been observed to be reversed in direction, are already present, their activity is generally intensified; but if the stomach be quiescent before vomiting commences, it may remain perfectly passive throughout. The pylorus is almost always firmly closed, so that but little of the food escapes into the intestine. The flow of bile is usually increased. The interesting observation was made by Rühle, that if a manometer be fastened into the stomach, and vomiting be excited, instead of an elevation there is a descent of the mercury, momentarily preceding the expulsion of the contents: this must doubtless be referred to the sudden and *active* opening of the cardiac orifice produced by the dilatator fibres described by Schiff, which occurs just antecedently to the pressure exerted by the muscles of the abdomen. There can be but little doubt that the violent but fruitless efforts at vomiting which we occasionally witness (two or three such

* Busch, Virchow's "Archiv," Band xiv. p. 166.

† Schiff has pointed out that for Magendie's experiment to succeed the cardiac orifice and lower part of the œsophagus must also be removed, the contraction of these parts otherwise preventing the escape of the contents of the bladder.

‡ Moleschott's "Unters.," Band x. 1867, p. 353.

§ Lepine, "Bullet. de l'Acad. Roy. de Méd.," 1844; and Patry, in "Allgem. Med. Centralblatt," 1863, No. 62.

efforts frequently preceding the effectual one), are prevented from emptying the stomach by the obstinacy with which the cardiac sphincter is kept closed; just as the expiratory effort which assists in emptying the stomach is prevented by the firmness with which the glottis is held shut, from expelling the contents from the chest. The immediate causes of vomiting may be reduced to several different categories. 1st. The contact of irritating substances with the mucous membane of the stomach itself; these, however, cannot act by *direct* stimulation upon more than its own muscular coat; and their operation upon the associated muscles must take place by *reflexion*, through the "nervous circle" furnished by the pneumogastrics and the motor nerves of expiration. 2nd. Irritations applied to other parts of the body, likewise operating by *simply-reflex* transmission; as in the vomiting which is consequent upon the strangulation of a hernia, or the passage of a renal calculus. 3rd. To the direct irritation of the nervous centres by certain irritants (Tartar Emetic, Apomorphin); and, perhaps we may add, the vomiting that occurs after division of *both* pneumogastrics—the division of one having but little effect.* 4th. Impressions received through the *sensorial* centres, which may be either sensational or emotional, but which do not operate unless they are *felt*. In this mode seems to be excited the vomiting that is induced by tickling the fauces, which first gives rise to the sensation of nausea; as well as the vomiting consequent upon disgusting sights, odours, or tastes, and upon those peculiar internal sensations which are preliminary to "sea-sickness." The *recollection* of these sensations, conjoined with the emotional state which they originally excited, may itself become an efficient cause of the action, at least in individuals of peculiarly irritable stomachs or of highly sensitive nervous systems; for this plays downwards upon the sensorial centres, in such a manner as to excite in them the same condition as that which was originally produced through the medium of the sensory nerve when the object was actually present. (See CHAP. XIII., Sect. 3.)

96. The passage of the Chyme, or product of the gastric digestion, through the pyloric orifice, into the commencement of the *Intestinal tube*, is at first slow; but when the digestive process is nearly completed, it is transmitted in

* This appears to be demonstrated by the experiments of Chouppe (Société de Biologie, Séance, 18 July, 1874), who observed that after section of both pneumogastrics in dogs, the intravenous injection of tartar-emetic and of apomorphin caused free vomiting, whilst Ipecacuanha or its active principle, Emetin, had no action; from whence the conclusion may be drawn that the two first-named drugs act on the vagal centre as well as upon the peripheric extremities of the vagi in the gastric mucous membrane, whilst the action of emetin seems to be confined to the latter. Hermann (Pflüger's "Archiv," Band v. 1872, p. 280) grounding his opinion on the result of an experiment made by Grimm (Idem, Band iv. 1871, p. 205), showing that tartar-emetic injected into the veins takes a longer time to act than when injected into the stomach, believes that this salt has a specific action on the parietes of the stomach; but it may be remarked that, as above stated, Magendie long ago showed that efforts to vomit followed the injection of tartar-emetic, after the ablation of the entire stomach. (See D'Ornellas' "Bulletin générale de Thérapeutique," 1873, p. 193 *et seq.*) D'Ornellas considers that vomiting may be produced by three kinds of efforts: 1, Intrinsic, or by the contraction of the stomach alone; 2, Extrinsic, or by the contraction of the expiratory muscles; and 3, by mixed or combined and co-ordinated, intrinsic and extrinsic efforts; and the nerves implicated may be either the pneumogastrics, the nerves of special sense, or the sympathetic. In meningitis, in cases of cerebral tumour, and in hæmorrhage, the feeling of nausea is probably conveyed by the sensory branches of the glosso-pharyngeal nerve. The nauseating principle of some drugs, though generally, is not always identical with that producing their emetic effect. Thus in the case of Ipecacuanha the nauseating principle is an odorous substance, capable of separation by ether, in which it is soluble, whilst the emetic principle is soluble in alcohol. The former can produce vomiting immediately on being swallowed, or even before by its action on the olfactory and glosso-pharyngeal nerves, whilst the latter acts as above stated on the vagal branches distributed to the stomach.

much larger quantities. The pyloric orifice, like the cardiac, is furnished with a sphincter muscle; but how far its contractions are dependent upon "reflex action" has not yet been ascertained. The ingested matter, which undergoes further changes of a very important character within this portion of the canal, is gradually propelled onwards by the peristaltic contractions of its walls; and these are excited by the contact, either of the products of digestion, or of the secretions poured in by the various glands that discharge their products into the intestinal tube.* In its progress along the small intestines, the nutritious portion of the ingested matter is gradually taken up by the blood-vessels and absorbents; and the residue, combined with excrementitious matters separated from the blood, begins to assume the fæcal character. A further absorption takes place during the passage of the fæcal matter through the large intestines; and thus by the time it reaches the rectum, it has acquired a considerable degree of consistency.

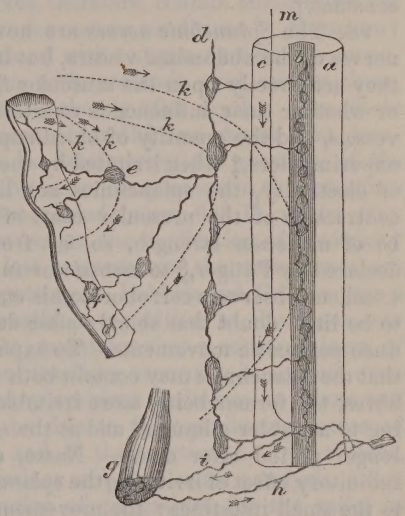
97. The nervous supply of the intestines is derived essentially from the sympathetic system; though some fibres may be derived from the pneumogastrics. The sympathetic fibres proceeding from the cœliac, mesenteric, and other plexuses accompany the blood-vessels to the intestines, and form a chain of nerves and nervous ganglia, the *Plexus myentericus*, one portion of which has been shown by Auerbach to lie between, and to supply both the circular and longitudinal layers of muscular tissue of the *small* intestines, and to be situated on the outside of the longitudinal layer in the *large* intestine, whilst another portion, discovered by Meissner, lies in the submucous areolar tissue, and is probably destined for the supply of the *muscularis mucosæ*, or muscular layer of the mucous membrane.† It might at first sight appear to be easy to determine the precise influence of the nervous system upon the muscular walls of the intestines, but experience has shown that the investigation is amongst the most difficult in experimental physiology, various results having been obtained according to the animal experimented on; the nature of the stimulus applied; the precise part stimulated; the state of distension of the tube; the fulness or emptiness of the blood-vessels; the venous or arterial condition of the blood circulating through the tissues, and the temperature at which the experiments are conducted. The inquiry is further complicated by the fact that the splanchnic nerves, which are the vaso-motor nerves of the vessels supplying the abdominal viscera, appear also, under certain circumstances, to exert an inhibitory influence on the intestinal movements. It may be certainly stated that in the fœtus, and during sleep, perhaps in consequence of the large relative quantity of oxygen contained in the blood in each of these states, and also when empty, the intestines are quiescent (*aperistalsis*), or at most their movements are extremely slow and feeble; but as soon as food is propelled

* The Bile seems to have an important share in producing this effect; since, when the ductus choledochus is tied, constipation always occurs. M. Legros and Onimus (Robin's "Journal de l'Anat.," 1869, pp. 37 and 163) have shown by tracings taken from a caoutchouc ball introduced into the intestines, that the peristaltic contractions move more rapidly in the duodenum (sometimes traversing 8 inches in the minute) than in the cæcum (6 inches) of the dog.

† Auerbach, Canstatt's "Jahresbericht," 1862, p. 174; Manz, "Die Nerven und Ganglien des Saugethierdarms," 1859; Krause, "Studien des Phys. Instit. zu Breslau," 1863, p. 41. "Unters. ub. einig. Ursach. der peristalt. Beweg. des Darmcanals;" and Virchow's "Archiv," 1864, p. 467. According to Gerlach (abstract in Humphry and Turner's "Journ. of Anat." vol. viii. 1874, p. 173) the myenteric plexus of Auerbach contains highly vascular ganglia and fasciculi of fibres, forming primary and secondary networks. From the secondary plexuses fine fibres arise, each of which ends in a corpuscle that may give off one or two processes, ending between the muscular fibres. Klein ("Q. J. of Mic. Sci.," Oct 1873) describes in addition to the above, isolated ganglion-cells, between the circular and longitudinal muscular coats.

into them from the stomach, peristaltic contractions commence, which force the contents onwards, and may become violent (*dysperistalsis*). These movements are of a reflex nature, the circuit consisting of centripetal sensory nerve-fibres distributed to the mucous membrane, which convey the impression produced by the presence of food to the ganglia of the plexuses of Auerbach and Meissner, from whence an impulse is reflected to the muscular tissues of the intestine, as may be understood from an examination of the accompanying wood-cut (Fig. 63). Coincidently with the entrance of food into the intestines, the blood-vessels become turgid with blood, a condition that appears greatly to heighten the irritability of the nervo-muscular apparatus, for stimuli which provoke no response when the vessels are comparatively empty, will produce well-marked effects when they are full.* A large amount of evidence has been accumulated, showing that the peristaltic movements may be influenced by distant cerebro-spinal and sympathetic centres, but the precise channels through which their influence is transmitted are still undetermined. Schiff† and Budge,‡ in experiments on cats, observed movements of the intestines follow stimulation of the *corpora striata*, *pons Varolii*, *medulla oblongata*, and other parts of the *encephalon*; and the remarkable influence of certain emotions, as fear, in increasing peristalsis, as well as the history of many pathological cases, supports the view that the cerebro-spinal nervous system can act more or less directly upon the intestines. Good evidence that the fibres by which irritation of the more remote sympathetic ganglia act upon the intestines are contained in the spinal cord, is afforded by the following experiment of M. C. Bernard:—The spinal cord is divided below the medulla oblongata, to abolish the influence of the Will. The chest is then opened, and the inferior cervical ganglion stimulated. After a few seconds, active movements of the small intestines takes place. The cord connecting the inferior cervical with the first thoracic ganglion is now divided, and the lower extremity stimulated. The intestines remain quiescent. But if the upper extremity be stimulated, active intestinal movements again occur.§ The *Pneumogastrics* are

Fig. 63.



Nervous supply of the *Intestines*.—*a*, is the posterior column of the spinal cord; *b*, the grey substance with its chain of ganglion cells; *c*, anterior column; *d*, great sympathetic; *e*, nervous ganglion of mesentery; *f*, ganglion of nerve plexus in the walls of the intestine; *g*, sphincter ani; *h*, sensory filament running centripetally to the ano-spinal centre by the posterior column; *i*, motor root with fibre, running centrifugally from the ano-spinal centre to the sphincter: *m*, encephalic fibre, conducting the mandates of the will to this centre; *k*, curves of successively wider and wider area showing the implication under stronger and stronger stimuli, of a progressively increasing number of ganglia, till the cord is at length reached, when pain and various reflex effects on distant parts may be experienced.

* Van Braam Houckgeest, Pflüger's "Archiv," 1872, p. 298.

† "Lehrbuch der Physiologie," 1859. ‡ "Lehrbuch der Physiologie," 1862, p. 785.

§ Experiments made like those of Pincus, Budge, Adrian, and Lamansky, with a view of determining the functions of the cœliac and mesenteric plexuses by noticing the effects of their ablation can scarcely be of any service, since the operation required is accompanied by much hæmorrhage and is so severe as to cause death in a few hours. However, the chief phenomena observed have been congestion, and ecchymoses in the mucous membrane of the stomach and small intestine, with hypersecretion of mucus, liquid fæces, and more or less severe peritonitis. M. Moreau, "Comptes Rendus," 1868, p. 554, has shown that section of the nerves supplying a fold of intestine leads to effusion into it.

believed by many to be also a channel by which impulses proceeding from the cerebro-spinal centres are transmitted to the intestines, since electrical excitation of these nerves usually, though not always, produces contractions which commence in the stomach, and are most evident when the splanchnics have been divided,* and also at a short interval after death. It must be admitted, however, that the effects of stimulating the pneumogastrics are very inconstant.†

98. The *Splanchnic nerves* are now well known to be the chief *vaso-motor* nerves of the abdominal viscera, but it is difficult to say whether, when irritated, they act directly upon the muscular fibres or nervous ganglia of the intestines, or whether their influence is exerted indirectly by modifying the size of the vessels, and the quantity of blood supplied to these parts. According to some experimenters,‡ when irritated by the application of exceedingly feeble currents of electricity, the splanchnics act like ordinary *motor* nerves, and produce contraction of the muscular coats of the intestine. If, however, the current be of moderate strength, so far from causing contraction, these nerves are declared by Pflüger,§ to *restrain* or *inhibit* the peristaltic movements, and many excellent observers corroborate his statements. On the other hand, there seems to be little doubt that shortly after death irritation of the splanchnics will produce peristaltic movements. To explain these phenomena, Nasse has suggested that the splanchnics may contain both motor and inhibitory as well as vasomotor fibres, the former being more irritable than the latter—that is to say, responding to a feebler stimulus, and at the same time retaining their irritability for a longer period after death. Nasse, experimenting on rabbits, found that the inhibitory effect of irritating the splanchnics immediately after death, was limited to the small intestines; the movements of the stomach, colon, and rectum remaining unaffected. The arrest of movement took place so quickly after the application of the stimulus to the nerves as to lead him to the conclusion that it was a direct effect, and not secondary to contraction of the blood-vessels. Kölliker states that the inhibitory power of the splanchnics is abolished by curare; and Brunton‖ was unable to perceive it in several animals narcotized by chloral. The splanchnics also contain *sensory* fibres.

99. The movements of the intestines appear further to be powerfully affected by the quantity of blood supplied to them, as well as by its arterial or venous quality. Nasse observed lively movements, both when the vessels were rendered anæmic by pressure on the aorta, and when blood was injected at a high pressure. S. Mayer and v. Basch¶ remark that compression of the thoracic aorta usually, but not always, causes vigorous contraction both of the longitudinal and circular muscular fibres of the intestines, which they attribute to the excitation

* Houckgeest, Pflüger's "Archiv," 1873, Band vi. p. 266.

† Legros and Onimus (Robin's "Journal de l'Anat. et de la Physiologie," 1869, p. 196) state that the application of interrupted currents of electricity to the pneumogastrics produces relaxation and immobility of the intestines, whilst continuous currents exert but little action upon them. Sanders Ezn (Humphry and Turner's "Journal of Anat." vol. vi. p. 242, 1872) states that irritation of the right pneumogastric chiefly causes movement in the duodenum, and irritation of the left, movement in the ileum. Goltz (Pflüger's "Archiv," 1872, p. 616) has shown that in the frog the excitability of the myenteric ganglia is very greatly augmented when, by destruction of the brain and spinal cord or section of the pneumogastrics, they are cut off from the central nervous system, which therefore in this animal appears to exert an inhibitory influence upon them.

‡ Lister, "Proceed. Roy. Soc.," 1858; Nasse, "Beiträge zur Physiologie der Darmbewegungen," 1866; "Wundt. Physiologie," 1873, p. 191.

§ See Ludwig and Spiess, "Sitzungsberichte d. k. Akad. der Wiss. zu Wien," Band xxv. 1857, p. 580; Kölliker; Houckgeest, Pflüger's "Archiv," Band vi. p. 266; and others.

‖ "Handbook for the Phys. Laboratory," 1873, p. 526.

¶ "Sitz. d. k. Akad. zu Wien," Band lxii. 1870 p. 809.

either of the peripheral extremities of the splanchnic and vagi, of the solar plexus, of the ganglia of the myenteric plexus, or possibly even of the muscular fibres themselves, by the carbonic acid or other product of disintegration, which accumulates in the stagnating blood. They maintain that when such products are present, lively movements can be induced by irritation either of the splanchnics or of the pneumogastrics; but that when absent, no amount of irritation of these nerves has any effect. Both nerves, therefore, contain motor fibres for the intestines, which, however, only act under certain conditions.* Hermann† remarks simply that saturation of the blood with oxygen arrests the movements of the intestines, whilst saturation with carbonic acid excites them, which explains to some extent their activity shortly after death. The whole subject requires to be reinvestigated, since Horvath‡ has shown that temperature has a very powerful influence in determining the reaction of the intestinal walls to electric stimulation. No movements occur in the intestines according to this observer, when they are cooled below 66° F., whilst they exhibit spontaneous movements, and contract on the application of electricity between 66° F. and 106° F., at which last temperature the movements are sometimes very vigorous and rapid, supporting in Rabbits and Guinea-pigs a column of water 18 cm. in height. Horvath, in opposition to the statements of Nasse, Legros, and Onimus and Mayer, maintains that a certain fulness of the vessels is absolutely necessary; no contractions occurring in anæmia even at a high temperature. The action of many aperient medicines, as Senna and Croton oil, has been demonstrated§ to be due to their producing increased peristalsis; if pushed too far, however, and if their action be very violent, they diminish the irritability of the intestines and even cause paralysis, a fact not to be overlooked in the administration of purgatives for the relief of constipation. Saline aperients, if given in a sufficient state of concentration, probably act chiefly by producing diosmosis; but partly also by causing increased secretion—not by increasing peristalsis.‖ Certain poisons excite lively intestinal movements. Nasse observed that injection of nicotin and of sulphocyanide of potassium caused violent tetanic spasms of the small intestines in rabbits. Opium acted but slightly, and strychnia and curare were totally inoperative. Carbonic acid intoxication caused general contraction, but no active movements of the walls of the intestines.

100. The rapidity with which the food traverses the intestinal tube is subject to great variations. A comparison of observations made on patients suffering from fistula in different regions of the alimentary canal shows that part of the food passes rapidly through the stomach into the intestines, but that having

* It is to be noted, however, that although the absence of arterial blood causes lively contractions, none are produced by an excess of venous blood in the mesenteric veins, such as may be occasioned by pressure on the vena portæ. This fact is admitted by Mayer and Basch, and has also been demonstrated by Legros and Onimus (Robin's "Journal de Physiol.," 1869, pp. 37 and 163). It should also be stated that Van Braam Houckgeest (Pflüger's "Archiv," 1872, p. 298), who operated carefully by opening the abdomen whilst the animals experimented on were immersed in water containing 0·6 of common salt, at blood heat, maintains that anæmic conditions prevent, arrest, or weaken the movements of the intestines, and that whilst distension of the vessels with *either* arterial or venous blood favours contraction in the *small* intestines, the latter condition alone seems to increase the irritability of the the nervo-muscular apparatus of the *large* intestines in Rabbits. Sanders Ezn (Humphry and Turner's "Journal of Anat.," vol. vi. 1872, p. 424), operating in the same way as Houckgeest, maintains that the amount of blood in the vessels has no influence on the intestinal movements.

† "Physiologie," 1874, p. 136. ‡ "Centralblatt f. d. Med. Wiss.," 1873, p. 597 *et. seq*

§ By Radziejewsky, "Archiv f. Anat. v. Physiolog." 1870; and Legros and Onimus, *loc. cit.*

‖ Legros and Onimus, *op. cit.*

reached the duodenum it traverses that and the following segments of the intestines comparatively slowly. Thus, in a case of duodenal fistula in a man, recorded by Kühne,* portions of uncoagulated milk, and small fragments of meat, were observed to make their appearance within ten minutes of their being swallowed. So, too, in a case of artificial anus which opened into the upper part of the jejunum, reported by Dr. Busch,† the first portions of food usually appeared in from 15 to 30 minutes after ingestion. But in another case reported by Dr. Braune,‡ in which the artificial anus communicated with the intestine a few inches above the ileo-colic valve, the first appearance of the food did not present itself earlier than two hours and a quarter after ingestion, and the last not until about six hours after, so that we may consider the time occupied by the food in traversing the small intestine, to be about 3 or 4 hours. The food having traversed the small intestine, enters the cæcum by an aperture guarded by a valve (the Ileo-cæcal), whose lateral position is clearly a provision for preventing the whole weight of the Fæces, as the remains of the food here begin to be called, by which it might be forced back, from resting upon it. The Fæces here propelled forwards more slowly are in their ascent lodged in the sacculi of the colon, by which they are supported during the intervals of the peristaltic action of the Muscular Coat. In their course through the descending colon, they pass through its remarkable sigmoid flexure, by which they are prevented from directly pressing against the anal orifice.§ According to the observations of M. Voit,‖ in cats and dogs the evacuation of fæces, known by their characters to proceed from particular kinds of food previously given, almost invariably occupies 24 hours.

101. On examining the outlet by which the fæces are voided, we find that it is placed, like the entrance, under the guardianship of a ganglionic centre described by Masius, termed the ano-spinal centre, situate in the lower part (opposite the 6th lumbar vertebra in the Rabbit) of the Spinal Cord; subject, however, to some control on the part of the will. In the lowest animals, the act of discharging excrementitious matter is probably as involuntary as are the acts immediately concerned in the introduction of nutriment; and it is performed as often as there is anything to be got rid of. In the higher classes, however, such discharges are much less frequent, as reservoirs are provided, in which the excrementitious matter may accumulate in the intervals. The associated movements required to empty these are completely involuntary in their character, and are excited by the quantity, or stimulating quality, of the contents of the reservoir. But, had volition no control over them, great inconvenience would ensue; hence, sensation is excited by the same stimulus which produces the movements, in order that, by arousing the will, the otherwise involuntary motions may be restrained and directed. There can be little doubt, from the experiments of Dr. M. Hall, as well as from other considerations, that the associated movements by which the contents of the rectum and bladder are discharged, correspond much with those of Respiration; being in their own

* "Physiologische Chemie," 1868, p. 53. † Virchow's "Archiv," Band xiv. p. 140.
‡ "Virchow's "Archiv," Band xix. p. 470, 1860.

§ For some further observations on Defæcation, the reader is referred to O'Beirne, "New Views of the Process of Defæcation," Washington, 1834; and to vol. ii. p. 406, of Dr. Austin Flint's "Physiology of Man," both of whom agree in believing that under ordinary circumstances the rectum is contracted and contains neither fæces nor gas, whilst the condition which immediately precedes the desire for defæcation is probably the descent of the contents of the sigmoid flexure of the colon into the rectum. They admit, however, that under certain circumstances fæces must accumulate in the lower and dilated portion of the rectum.

‖ "Zeits. f. Bilogoie," Band ii. p. 6.

nature excito-motor, but being capable of a certain degree of voluntary restraint and assistance. The act of Defæcation (as of Urination) chiefly depends upon the combined contraction of the abdominal muscles, similar to that which is concerned in the expiratory movement; but, the glottis being closed so as to prevent the upward motion of the diaphragm, their force acts only on the contents of the abdominal cavity; and so long as the sphincter of the cardiac orifice of the stomach remains closed, it must press downwards upon the walls of the rectum and bladder—the contents of the one or the other of these cavities, or of both, being expelled, according to the condition of their respective sphincters. These actions are doubtless assisted by the contraction of the walls of the rectum and bladder themselves, for we sometimes find their agency sufficient to expel the contents of the cavities, when there is a total paralysis of the ordinary expulsors, provided that the sphincters be at the same time sufficiently relaxed.* This is more especially the case when their power is augmented by increased nutrition. For example, in many cases of disease or injury of the Spinal Cord the bladder ceases to expel its contents, through the interruption of the circle of reflex action; but after a time, the necessity for drawing off the urine by the catheter is found to exist no longer, the fluid being constantly expelled as soon as it has accumulated in small quantities. In such cases, the mucous coat is found after death to be thickened and inflamed, and the muscular coat to be greatly increased in strength, and contracted upon itself. It would seem, then, that the abnormal irritability of the mucous membrane, dependent upon increased development and activity of local ganglionic centres, and the increased nutrition of the muscular substance which appears consequent upon this, enable the latter to expel the urine without the assistance of the ordinary expulsors.

102. On the other hand, the sphincters which antagonize the expellent action are usually maintained in a state of moderate contraction, so as to afford a constant check to the egress of the contents of the cavities; and this condition has been fully proved to result from their connection with the lower part of the Spinal Cord, ceasing completely when this is interrupted. But the sphincters are certainly in part controlled by the will, and are made to act in obedience to the warning given by sensation; and this voluntary power is frequently destroyed by injuries of the Brain, whilst the Spinal Cord remains able to perform all its own functions, so that discharge of the urine and fæces occurs. In their state of moderate excitement, the expulsors and the sphincters may be regarded as balancing one another, so far as their reflex action is concerned, the latter having rather the predominance, so as to restrain the operation of the former. But, when the quantity or quality of the contents of the cavity gives an excessive stimulus to the former, their action predominates, unless the will be put in force to strengthen the resistance of the sphincter; this we are frequently experiencing, sometimes to our great discomfort. On the other hand, if the stimulus be deficient, the will must aid the expulsors, in order to overcome that resistance which is due to the reflex contraction of the sphincters; of this also we may convince ourselves, when a sense of propriety, or a prospective regard to convenience, occasions us to evacuate the contents of the rectum or bladder without a natural call to do so.

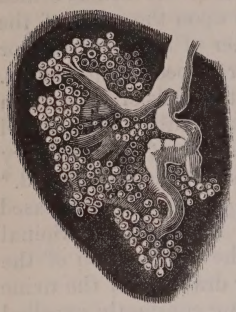
4. *Of the Changes which the Food undergoes during its passage along the Alimentary Canal.*

103. The object of the Digestive process, as already pointed-out, is to reduce the Alimentary matters to a condition in which they can be introduced

* A special sphincter has been described by Chadwick ("Gynæcolog. Trans.," 1877, vol. ii. which acts as a detrusor.

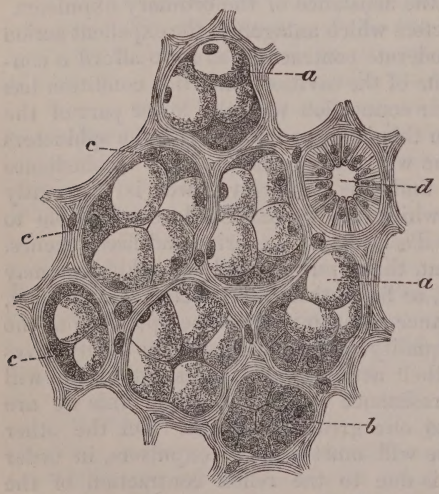
by Absorption into the Circulating system. This reduction is partly effected, as we have seen, by Mechanical means; but it is chiefly due to the Chemical agencies which are brought to bear upon the ingested substances, during their transit through the mouth, the stomach, and the upper portion of the intestinal tube. The first of these is exerted by the *Salivary* fluid, which is incorporated with the food in the act of mastication, and of which a large quantity descends with it to the stomach. For the secretion of this fluid, it will be remembered that three pairs of glands of considerable size are provided—namely, the parotid, the submaxillary, and the sublingual. But in addition to these there is a small pair situated just at the tip of the tongue, whilst a very important part of the fluid is furnished by the lingual and palatine glands, and by the numerous follicular glands lodged in and beneath the buccal mucous membrane. The larger Salivary glands are all constructed upon the type of compound racemose glands, the principal features of which are shown in Figs. 64 and 65. The excretory ducts (*d*, Fig. 65), which are lined by columnar epithelium, divide and subdivide till they terminate in a series of follicles, which contain, especially in the submaxillary gland, large centrally-situated transparent cells with flat and eccentric nuclei (*a*, *a*); and, in addition, a mass termed the "semilunar body of Giannuzzi" (*c*),* which appears at first sight to be granular protoplasm with interspersed nuclei, but which later investigations have shown to be composed of many closely-compressed cells in a condition of active growth. The central cells contain mucin, and their nuclei alone stain with carmine. The peripheric cells are albuminous, and both their bodies and their nuclei are thoroughly and completely stained with carmine.† It is believed that the albuminous cells during the period of rest of the gland gradually become metamorphosed, and develop into the mucin-holding cells, which break down or yield up their contents during the period of active secretion, the latter in the meanwhile growing, so as to fill the acinus when the gland is exhausted with dark granular protoplasmic cells. In glands which secrete saliva containing little or no mucin, like those of the rabbit and the parotid of the dog, peripheral cells only are present; and even in the submaxillary gland of the dog there are many acini which contain no central

Fig. 64.



Lobule of *Parotid Gland* of new-born infant, injected with mercury. Magnified 50 diameters.

Fig. 65.



Submaxillary gland of the dog.—*a*, mucus cells; *b*, protoplasm cells; *c*, semilunar body of Giannuzzi; *d*, transverse section of an excretory duct, with its peculiar columnar epithelial cells.

* "Bericht d. Sächs Gesellsch. d. Wiss.," 1866, p. 68.

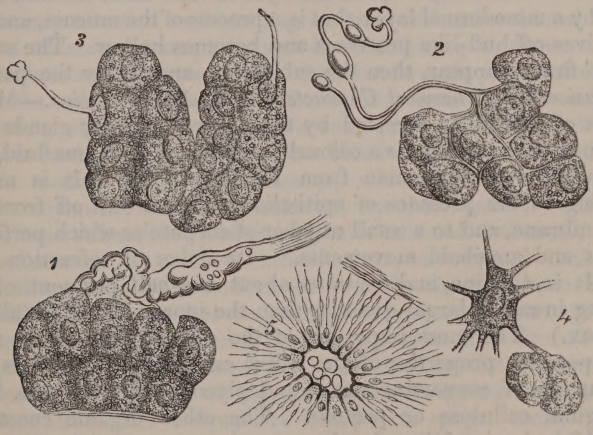
† Heidenhain, "Studien des Physiolog. Institut. zu Breslau," 1868, Heft 4.

or mucin-holding cells.* Bermann† finds a second gland constructed on the compound tubular type in the submaxillary gland of man and of the rabbit. The ducts are looped and tortuous and open into Wharton's duct, and in a late communication‡ he maintains that in the submaxillary gland of the mouse, bat, cat, and dog, there are three differently constructed glands combined: a true acinous gland; a compound tubular gland with tortuous canals, which are lined by a single layer of epithelium, and have no "semilunar bodies;" and lastly, a simple tubular gland.§ Ewald and others have observed a fine plexus surrounding the individual cells, which they believe to be the origin or ultimate termination of the Salivary ducts.‖ The follicles are surrounded by a rich plexus of blood-vessels, the interstices of which form spaces from which the lymphatics take origin. Pflüger¶ believes he has been able to follow nerve-fibres into direct continuity with the cells lining the acini and ducts of the salivary glands, and describes no less than four modes of termination. In the first (1 and 2,

Fig. 66.

Capillary Network around the Follicles of the *Parotid Gland.*

Fig. 67.



Modes of *Termination of the Nerves in the Salivary Glands.*—1 and 2, branching of the nerves between the salivary cells; 3, termination of the nerve in the nucleus; 4, union of a ganglion cell with a salivary cell; 5, varicose nerve-fibres entering the cylindrical cells of the excretory ducts.

Fig. 67), a cerebro-spinal nerve-fibre loses its sheath as it passes through the basement membrane of the acinus, with which the sheath becomes

* Pflüger, Schultze's "Archiv," Band v. p. 203.

† "Centralblatt f. d. Med. Wiss.," 1877, No. 50, p. 897. ‡ Idem., 1878, p. 718.

§ Nüssbaum believes that the cells secreting ferment may be distinguished from mucin-cells and from the substance of the gland by the deep brown tint they assume when exposed to the action of osmic acid (Schultze's "Archiv," Band xiii. p. 724). J. N. Langley, on the other hand, denies the correctness of the above statement (Kühne's "Untersuchungen," Band i. 1878, p. 471). See also Grot, in Hofmann's "Jahresber" for 1876, Band v. Th. i. p. 312.

‖ Boll has described an intra-alveolar reticulum of connective tissue, which is perhaps identical with it.

¶ Pamphlet, "On the Terminations of the Secretory Nerves of the Salivary Glands," 1866; and "Medicin. Centralblatt," Nos. 10 and 14, 1866; Kupffer, in Ludwig's "Festgabe," 1875, p. 64; see also Palladino (Abstract in "Centralblatt," 1873, p, 782), who, however,

continuous, whilst the medulla passes on between the gland-cells and divides into finer fibres, each of which, regaining a sheath, perforates the wall of one of the secreting cells and terminates in the nucleus. In the second mode (4, Fig. 67), the nerve-fibres, which probably belong to the *sympathetic system*, terminate in multipolar ganglion cells, some of the offsets or caudate prolongations of which in like manner penetrate the secreting cells and terminate in the nuclei. In the third mode (3, Fig. 67), a nerve-fibre, invested with a sheath containing nuclei, within which are numerous varicose axis cylinders covered by a thin layer of medullary substance, terminates peripherically in a conical enlargement, which he terms a "protoplasma-foot or expansion," and which he regards as a kind of intermediate organ between the nervous and glandular substance. Lastly, he has observed certain nerve-fibres distributed to the cylindrical cells lining the salivary ducts (5, Fig. 67). The attached extremity of these cells is often marked with longitudinal striæ, and is continued for some distance as a varicose prolongation. The nerve-fibres lie beneath the basement membrane, and form exquisitely fine threads, with swellings or varicosities upon them, which he has been able to trace into direct continuity with the above-mentioned prolongations of the epithelial cells, several passing into each cell. The development of the salivary glands commences during the second half of the second month, by a simple solid protrusion of the deeper epithelial layer of the wall of the oral cavity which is invested by a mesodermal layer, that is, a process of the mucosa, and which subsequently gives-off bud-like processes and becomes hollow. The submaxillary gland is the first to appear, then the sublingual, and finally the parotid.

104. *Physical and Chemical Characters of the Mixed Saliva.*—Mixed saliva, the product of the fluids secreted by the several salivary glands and of the mucous glands of the mouth, is a colourless, ropy and spumous fluid, the specific gravity of which varies in man from 1·002 to 1·009. It is more or less cloudy, owing to the presence of epithelial scales thrown off from the buccal mucous membrane, and to a small number of corpuscles which perform curious spontaneous and amœboid movements.* Its index of refraction for light is 1·3354.† It is alkaline, and contains about one-half per cent. of solids, the organic being in rather larger quantity than the inorganic. (For fuller analysis, see APPENDIX.) The most important of the organic substances, and that on which the peculiar properties of the saliva essentially depends, is a *diastatic ferment*,‡ capable of converting starch and glycogen into glycose, but without action on gum, cellulose or pectose. The other organic constituents are *globulin*, which is precipitated when a current of carbonic acid gas is transmitted, and *mucin* with a trace of *albumin*, which renders the fluid cloudy on the addition of nitric acid after the removal of the globulin. The inorganic constituents are chiefly sodium chloride, sodium and calcium carbonates, with phosphates of potassium, sodium, calcium, and magnesium. There are also traces of nitric acid (Schonbein) and of potassium sulphocyanide, the quantity of

was only able to trace *non*-medullated nerve-fibres into the secretory cells of the submaxillary gland in the Horse. Asp (Abstract in "Centralblatt," 1873, p. 565), Mayer, Hering, Krause, Schweigger-Seidel, Henle, Klein, Ewald, and many others, express grave doubts as to the accuracy of Pflüger's statements of the mode of termination of the nerves in the salivary glands, and the subject may be regarded as being still sub judice.

* Brücke, "Sitzber. d. Wiener Akad.," Band xlv.

† Valentin, Pflüger's "Archiv," Band xix. p. 84.

‡ This was formerly termed *ptyalin*, but Hoppe-Seyler recommends the use of the term to be discontinued, as it has been applied to different substances. It is either altogether absent, or exists only in small quantities in the saliva of dogs and horses, but is abundant that of the rabbit and guinea-pig. ("Phys. Chem.," 1868, p. 186.)

the latter amounting to about 0·16 per 1000,* the use of which may possibly be as suggested by Kletzinsky† to prevent the development of bacteria and other low organisms between and in the cavities of the teeth. It appears to be absent in the dog. Though always alkaline when it is being secreted in health, the mixed saliva becomes neutral or even acid if long retained in the mouth, and is often acid in advanced stages of diabetes. It contains a certain quantity of free gas, one hundred cub. cent. of the saliva of the dog yielding about 0·5 per cent. of its volume of oxygen, about 0·7 per cent. of nitrogen, and about 20 per cent. of carbonic acid gas to a vacuum, whilst nearly double that quantity is eliminated on the addition of phosphoric acid.‡

The secretion of the several salivary glands presents well-marked peculiarities both in physical and chemical characters, as was first demonstrated by Claude Bernard, who inserted tubes into the different ducts, and found on placing a few drops of vinegar on the tongue of a dog that the submaxillary saliva was immediately secreted, speedily followed by that from the parotid, and at a later period by that from the sublingual. The fluid discharged by the parotid gland was clear and watery, that of the sublingual thick and viscid, whilst that of the submaxillary was intermediate in this respect to the others. Hence Bernard was led to suggest that the submaxillary gland ministers to the sense of taste, whilst the parotid is subservient to mastication and the sublingual to deglutition. *Submaxillary saliva* is distinctly alkaline, and has a sp. gr. of 1·005, a considerable quantity of mucin, and is active, except in new-born children, in converting starch-paste into dextrin and ptyalose. The diastatic ferment does not appear in it until about the end of the second month, and hence it is unadvisable to give very young children much amylaceous food. Metallic iodides which have been absorbed or injected into the blood appear in the submaxillary saliva in the course of a few minutes, whilst other metallic salts, as potassium ferrocyanide, are not eliminated by this channel. After standing for some time submaxillary saliva deposits calcium carbonate, with some albuminous substance. *Parotidean saliva* is clear, watery, and distinctly alkaline. It contains a little diastatic ferment even in the new-born child,§ and sulphocyanide of potassium, but no mucin, or if any, only traces from minute muciparous glands, which Bernard‖ has shown open into Steno's duct as it traverses the cheek. It presents great variations in the proportions of its solid constituents, the amount of inorganic matter varying more than double, and of organic substances twenty-five-fold.¶ Its sp. gr. varies from 1·0061 to 1·0088. The size of the parotid gland in animals is proportionate to the degree in which the mastication of their food is performed. It is large in the horse, which lives on comparatively dry food, less in Carnivora, and still less in the aquatic mammals. It is absent in birds, which swallow their food whole.** The extreme ropiness of *sublingual saliva* is due to the large amount of mucin present in it. Heidenhain found that it contained 2·75 per cent. of solids. The submaxillary gland is largely developed in the Carnivora, but is

* According to Vierordt, "Anwendung des Spectral Apparat. zur Photometrie," 1873, p. 147, who estimated its amount by measuring the absorption of light in the green and blue portions of the red fluid produced on the addition of iron chloride to the saliva. See also Bernard, "Leçons," 1859, t. ii. p. 243.

† Heller's "Archiv," 1833, p. 39. ‡ Pflüger's "Archiv," 1868, Band i. p. 688.

§ Zweifel, quoted in Hoppe-Seyler, "Phys. Chemie," 1878, p. 199.

‖ "Leçons de Physiologie Operatoire," 1879, p. 509.

¶ Heidenhain, Pflüger's "Archiv," Band xvii. p. 22. See also Bidder and Schmidt. "Die Verdauungs-säfte," 1852, p. 7; and Herter in Hoppe-Seyler's "Phys. Chemie," 1878, p. 199.

** Bernard, "Revue Scientifique," 1873.

reduced to a minimum in Birds. In Fishes the larger glands are wholly absent.*

105. Of the quantity of Saliva which is secreted daily it is impossible to form an exact estimate, since it varies greatly with the character of the food ingested, and the frequency with which that food is taken; the secreting process being, indeed, almost suspended when the masticating muscles and tongue are completely at rest, unless excited by a nervous stimulus. The taste, the sight, or even the idea, of savoury food, is sufficient to cause a flow of saliva, especially after a long fast: but it is by the masticatory movements that this flow is chiefly promoted, so that the amount poured-forth will in a great degree depend upon the duration of these movements,—this, again, being governed by the degree in which the food requires mechanical reduction. Harley, with great probability, estimates it at from 1 to 2 lbs. in man. Oehl found the quantity obtained by catheterization from the submaxillary gland, as compared with the parotid, to be as 3 : 1. He obtained 26 grains per hour from a fasting man, and only 15 grains after food had been taken. The influence of the kind of food upon the quantity secreted was well shown by Tuczek,† who found that in adult men, fed exclusively on black bread, the amount of saliva secreted per diem was about 19, with white bread 24 oz., with mixed food 17 oz. With mixed food in an old man the amount was 13 oz., in an old woman 8 oz., and with the same in a child aged 1½ years 5 oz.‡ The influence of sapidity on the amount of saliva is shown by an experiment made by Dr. Dalton,§ in which it was found that meat gained 48 per cent., whilst bread, though so much drier, only gained 55 per cent. of its weight. In M. Oehl's experiments, Salt, Pepper, Vinegar, and Quinine excited the flow of saliva from the parotid and submaxillary glands to about an equal degree. Honey chiefly effected an increase of the submaxillary saliva. Butler Stoney‖ found in a woman with parotid fistula, that the flow of saliva from this gland was stimulated by mastication alone, but much more by the mastication of any sapid substance, especially if acid (tartaric acid). As compared with other glands, the salivary glands perform a large relative amount of work, secreting in the course of one hour, when in full activity, thirteen times their own weight of saliva.¶

106. *Uses of the Saliva.*—Besides the preparation of the food for the ulterior changes which it has to undergo, by promoting its mechanical reduction in the act of mastication, and by facilitating the subsequent admixture of other watery fluids, and besides the material assistance which it affords to the act of deglutition, the Saliva fulfils other and perhaps still more important purposes. Without its solvent action on many of the solid constituents of our food, their taste would be either greatly diminished in intensity or altogether lost. Moreover, by lubricating the surfaces of the mouth and teeth, it prevents the

* Heidenhain ("Ueber die Acinosendrüsen der Schleimhaut, &c., Inaug. Diss.," Breslau, 1870), and more recently Lavdowsky ("Zur feineren Anat. der Speicheldrüsen," Max Schultze's "Archiv," Band xiii. Heft 2), relying on certain peculiarities of the epithelial cells in the cul-de-sacs of the salivary glands, have distinguished two groups which they have named respectively the *mucous* and the *serous* salivary glands. Lavdowsky gives the following classification: *mucous glands*, orbital and suborbital (dog and cat); sublingual (dog, cat, rabbit, and man); *serous glands*, orbital and submaxillary (rabbit); parotid (dog, cat, rabbit, and man).

† "Zeitschrift f. Biologie," Band xii. p. 534.

‡ Lassaigne found on abstracting the Bolus of food, as it passed down the œsophagus in Horses, that 100 parts of green stalks were mingled with 49 parts of saliva, the same quantity of oats and barley with from 113 to 186 parts, and of dry hay with 406 parts of saliva. ("Comptes Rendus," xxi. p. 362.)

§ "Human Physiology," 1876, p. 147.

‖ Humphry and Turner's "Journ. of Anat. and Phys.," 1873, vol. vii. p. 161.

¶ Tuczek, "Zeitschrift f. Biologie," Band xii.

adhesion of viscid substances, whilst its presence is of great importance in enabling the tongue to perform the rapid movements requisite for distinct articulation, as is clearly indicated by the thick and almost unintelligible utterance of those in whom from any cause the mouth and tongue have become dry and parched. Lastly, it has a powerful chemical action upon the farinaceous constituents of food, the influence being of the nature of a ferment, so that a small proportion of Ptyalin will convert a considerable, though, according to Paschutin,* not an indefinite quantity of starch into "ferment" sugar. Starch submitted to the action of saliva is first converted into *erythrodextrin*, which is a substance that is stained red by tincture of Iodin, and then into *achroodextrin*, which is not coloured by iodin and sugar; and finally the achroodextrin is converted into sugar, a portion, named *dystropodextrin*† long resisting the action. The sugar thus formed, for which the name "ptyalose" has been proposed, to distinguish it from "glycose" and "maltose,"‡ has only half the power of reducing copper oxide possessed by glycose, whilst it refracts polarized light more strongly. Seegen found about 65 to 70 per cent. of glycogen is converted into ptyalose. If the starch be crude or raw the time required is considerable,§ amounting to two or three days even at blood heat, but the rapidity with which it takes place under favourable circumstances is very great; thus Vintschgau‖ found that if well boiled, thin starch-paste, which had been rendered blue by the addition of Iodin, were added drop by drop to Saliva at a temperature of 98° or 99° F., the colour instantly disappeared; and Dr. Dalton¶ found traces of sugar in starch-paste which had been kept in the mouth within 30 seconds. The action on glycogen is much more slow, and Lawilski** maintains that the salivary diastase has no power of converting pure dextrin into sugar. The temperature at which the action is most intense is at 95° F.,†† or if diluted with ten times its volume of water at a somewhat higher temperature, as from 100°·4 F. to 105°·8 F.,‡‡ whilst it becomes inoperative at 140° F. This power is not peculiar, however, to the Saliva; for Bernard has shown that it is possessed by many azotized substances in a state of incipient decomposition. The presence of a diastatic ferment has been ascertained in man in the saliva secreted by all the glands; but in the dog it is absent in the parotidean fluid, and it exists only in small quantities in the secretion of the other salivary glands, which is in accordance with the nature of the food of this animal. In man, the transforming process is certainly not checked on the passage of the food into the stomach, as it is in the dog, which is partly owing to the larger proportion of Ptyalin his saliva contains, and partly to the acidity of the gastric juice being much less. It would appear that the Saliva has little or no chemical action on either the oleaginous or on the azotized constituents of the food, and its operation on them, if it have any, must therefore be purely physical.

107. *Action of the Nerves upon the Salivary Glands.*—The relations of the nervous system to the salivary glands are peculiarly interesting, and on account of the proximity of these glands to the surface, and the facility with which heir nerves, vessels and ducts can be isolated, they have been studied with

* "Centralblatt," 1871, p. 372. † δυσροπος, obstinate.

‡ O. Nasse, Pflüger's "Archiv," Band xiv. 1877, p. 473; and J. Seegen, idem., Band xix. 1879, p. 122.

§ Schiff, "Physiologie de la Digestion," 1867, p. 153.

‖ "Atti del Instituto Veneto," t. iv. 1859. ¶ "Human Physiology," 1876, p. 142.

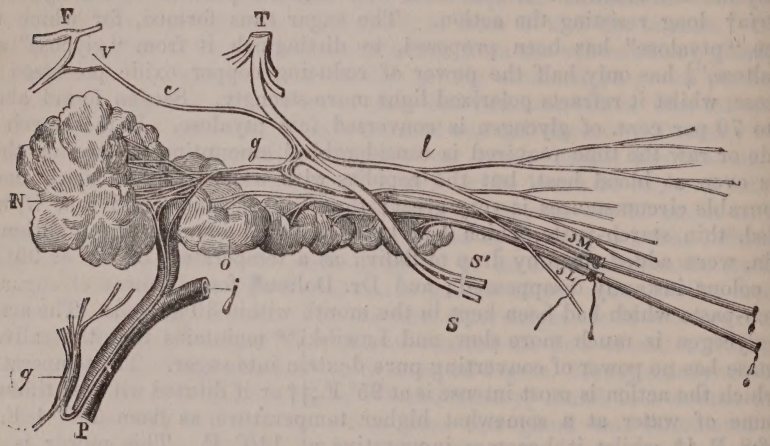
** Virchow, Hirsch. "Jahresber," 1874, Band i. p. 221.

†† Kühne, "Lehrb. d. Phys. Chemie," pp. 20, 21.

‡‡ Paschutin, "Centralblatt," 1870, p. 577.

great care by many observers.* In the case of the submaxillary and sublingual glands the sensory or centripetal nerves implicated are the fibres of the Glosso-pharyngeal and of the Fifth pair of nerves, and the secreto-motor, or centrifugal fibres, are branches of the Facial, the fibres of which run in the chorda tympani. In the case of the parotid gland, whilst the sensory channels are the same, the secreto-motor fibres run in the nervus petrosus superficialis minor, from the Facial to the otic ganglion, and then in the auriculo-temporal branch of the Fifth. The centre of reflection is the ganglionic mass in the medulla oblongata corresponding to the nuclei of origin of the Facial and Glosso-pharyngeal nerves. All the glands are supplied, in addition, with sympathetic

FIG. 68.



The *Submaxillary* and *sublingual glands* of the dog, with the nerves and vessels in relation to the submaxillary gland; to show the mechanism of the secretion in this gland.

N, submaxillary salivary gland; O, sublingual; JM, Wharton's duct: JL, duct of sublingual, each with a canula tied into it; T SS′ lingual branch of the inferior maxillary division of the Fifth nerve; SS′, branches distributed to the mucous membrane of the mouth; F, facial nerve; *c*, chorda tympani; *a*, branch of the Facial distributed to the submaxillary gland after running for a short distance with the lingual of the Fifth; *g*, submaxillary sympathetic ganglion; *q*, superior cervical ganglion; P, branch from this ganglion to the submaxillary gland; *j*, internal maxillary artery; V, vidian nerve; *l*, branch of the lingual nerve ramifying in the buccal mucous membrane.

or vaso-motor fibres, regulating the calibre of the vessels, the ganglia of which are the submaxillary and the sublingual ganglia† for the glands of the same name, and the otic for the parotid. In addition to the vaso-motor fibres, the sympathetic nerves supplying the submaxillary and sublingual glands appear to contain fibres which are secreto-motor, and excite a special kind of secretion. The influence of the nerves may be demonstrated by the following experiments:—If the submaxillary and sublingual glands be cleanly dissected out, they may be seen at rest, secreting little or no saliva, whilst the venous blood returning from them is of a dark tint. If a drop of vinegar be now placed upon the tongue of the animal, the arterial twigs supplying the gland immediately enlarge, the rapidity of the current of blood is increased, the veins pulsate and convey scarlet blood, the pressure of which on their inner

* Bernard (Lectures, "Med. Times and Gaz.," vol. i. 1860, pp. 288–361), Ludwig ("Lehrbuch der Physiologie," Band ii.), Eckhard ("Beiträge," Band ii. p. 205; iii. 1862, p. 41; iv. 1867, Heft 2), Schiff ("Physiologie," 1859, p. 393), Von Wittich (Virchow's "Archiv," Band xxxvii. and xxxix.), Bidder (Reichert and Dubois-Reymond's "Archiv," 1866, p. 339), and Heidenhain, *loc. cit.*

† Some observers, as Sappey, regard the so-called sublingual ganglion to be only a plexus.

surface is considerably increased, and there is an abundant* discharge of limpid, highly-alkaline saliva, containing small quantities of albumin, globulin and mucin. The evidence that these conditions, in the case of the submaxillary and sublingual glands, are the result of the stimulus of impressions transmitted through centripetal fibres of the Fifth and Glosso-pharyngeal nerves to the Medulla oblongata, and there reflected to the glands through centrifugal nerves contained in the chorda tympani, the saliva thus discharged being termed *chorda tympani saliva*, lies in the fact that if the sensory nerves be divided, gustatory impressions no longer cause a flow of saliva, whilst if the *central* or *proximal* cut extremities of the divided nerves be stimulated, an abundant flow is immediately induced. In like manner, after section of the Facial or of the Chorda tympani—which are the secreto-motor nerves—the vessels distributed to the submaxillary and sublingual glands contract, owing to the unopposed action of the sympathetic, the current in them becomes slower, the blood they contain darker, the secretion of Saliva diminishes, and vinegar placed on the tongue no longer excites the secretion; whilst, if the *distal* cut extremities of these nerves be stimulated, all the former phenomena recur. On the other hand, if the sympathetic branches proceeding to the submaxillary and submental glands from the plexus around the facial artery, and primarily from the superior cervical ganglion, be directly irritated, the current of blood becomes very slow in consequence of the contraction of the vessels, its colour in the veins very dark, and the secretion of Saliva, whilst it diminishes in quantity, becomes at the same time cloudy and remarkably viscous, contains more albumin and mucin, and a remarkable number of sarcode-like bodies possessing the power of spontaneous movement, but no increase of inorganic substances.† To this kind of Saliva the term *sympathetic saliva* has been applied. The influence of the sympathetic is regarded by Heidenhain‡ as essentially trophic. That the secretion does not wholly cease after section of the chorda tympani is believed by Bernard to be due to the reflex action of the submaxillary ganglion, but even when the sympathetic fibres are divided, it is not entirely stopped, a small quantity of so-called *paralytic saliva* continuing to be secreted when the tip of the tongue is excited by induced electricity. It is remarkable that if a little atropin be injected into the veins of an animal, stimulation of the chorda tympani is not followed by increased secretion of Saliva, though the dilatation of the blood-vessels occurs as usual. Hence it has been concluded that the Facial nerve contains two kinds of nerve-fibres—one, stimulating the cells to secrete, and the other, acting as dilating or inhibitory fibres upon the blood-vessels.

108. In the case of the parotid gland, the sensory nerves are of course the same as before, but the secreto-motor nerve is the lesser superficial petrosal nerve, for section of this nerve or of the auriculo-temporal branch of the Fifth pair, which the petrosal enters, arrests the secretion of the gland, whilst stimulation of the root of the facial or of the smaller petrosal or auriculo-temporal nerve causes an abundant flow of thin saliva, resembling that secreted by the submaxillary gland when the chorda tympani is stimulated, the vessels enlarging so much that they convey quadruple the amount of blood. The relations of the parotid to the sympathetic differ from those of the submaxillary

* 856 grains in one hour in a dog (Ludwig).

† The secretion that is discharged when a stimulus of gradually increasing intensity is applied to the sympathetic becomes progressively more abundant, and at the same time contains more organic constituents, though if the stimulation be rendered yet stronger, or be simply maintained at a high degree, the saliva becomes thin and limpid and poor in organic constituents.

‡ Pflüger's "Archiv," Band xviii. 1878, p. 1.

and sublingual glands, its stimulation merely causing a diminution in its quantity without effecting any change in the viscidity of the saliva secreted. It is possible that the otic ganglion may be the centre of reflexion without the cerebro-spinal centre being in any way implicated, the sensory impression passing by the Glosso-pharyngeal and the nervus petrosus superficialis minor, and being reflected at the ganglion upon the gland through the auriculo-temporal. Eckhard* maintains that in the *sheep* the Parotid glands act uninter-mittingly, and are not under the influence of any cerebral nerve, since no change was effected in the secretion by stimulation of the fifth, or of the portio dura of the seventh, or of the sympathetic nerve. Division of this last in the neck was also devoid of influence, and no increase in the quantity discharged was produced by brushing the mucous membrane of the mouth with vinegar. An extremely important point in the physiology of secretion has been pointed out by Ludwig, which shows the *direct influence of the nervous system* upon gland tissue and cells apart from any action on the blood-vessels, and that the process of secretion is not one of mere filtration; that if the circulation be suppressed either by ligature of the vessels or by decapitation of the animal, and either the sensory or excito-secretory nerves be irritated, Saliva may still be secreted. He also observed a fact which tells in the same direction—namely, that the pressure under which the saliva is secreted by the submaxillary glands as measured by a canula attached to a manometer, and introduced into Wharton's duct, is greater than the pressure of the blood in the carotids. In the former amounting to 190 mm. of mercury (or nearly 8 inches), whilst in the latter it was only 108·5—112·3 mm. (or about 4½ in.); and lastly he noticed that the temperature of the saliva was 1°·5 C., or nearly 3° F. warmer than the blood of the Carotid artery, a circumstance indicating that active chemical changes are taking place in the gland. The partial *independency* of secretory activity upon increased flow of blood through the gland is further shown by the experiments of Giannuzzi,† in which the glands were paralyzed by the injection into the ducts of a 4·9 per-cent. solution of Carbonate of Soda, or of a 0·5 per-cent. solution of hydrochloric acid. On stimulating the chorda tym-pani all the ordinary vascular phenomena made their appearance, but no increase in the amount of saliva secreted occurred and the gland soon became œdematous, the fluid which should have been used up in the formation of saliva apparently accumulating in the lymphatic system. Obviously, there-fore, secretion is not a purely physical action; and as Ranke‡ remarks, although a large supply of blood affords abundant material for secretion, it is requisite before this act can be accomplished that some change should occur in the gland cells themselves, which it is the special province of the nervous system to induce.§

* Henle and Pfeuffer, "Zeits.," Band xxix. 1867, Heft 1, p. 74.

† "Ber. d. k. sachs Gesells. d. Wiss.," 1865, p. 68.

‡ "Grundzüge der Physiologie," 1868, p. 181.

§ It would appear that there are well-marked differences in different animals in regard to the innervation of the salivary glands. In the *cat*, according to Langley ("Journal of Physiology," vol. i. 1878, p. 96), the effects of stimulation of the nerves are the opposite of those in the dog, the sympathetic secretion being more watery than that of the chorda tympani; the secretory function of the sympathetic nerve as well as that of the chorda being paralyzed by atropin; whilst thirdly, the sympathetic and chorda are not antagonistic for minimal effective stimuli, the apparent antagonistic action of the sympathetic on the chorda for maximal stimuli being probably due to a diminution of the blood supply. It seems, too, either that differences exist between the submaxillary gland of different rabbits or between the gland at different times, since Nüssbaum finds a diastatic ferment constantly present in it, whilst both Grützner and Schiff have been unable to recognise this ferment, either in the extract or in the secretion (Nüssbaum, Schultze's "Archiv," Band xiii. p. 724, and P. Grützner, Pflüger's "Archiv," Band xvi. 1877, p. 105). Perhaps, however, as Grützner suggests,

Heidenhain* has described at length the changes which take place in the salivary glands which have been excited to secrete for a considerable time by irritation of their nerves. These changes consist in the breaking down of the large mucin-holding salivary cells to furnish the secretion, and their replacement by a growth of small granular cells, which he believes to take place from the protoplasmic "semilunar" body of Giannuzzi (*c c*, Fig. 65); Ranvier,† however, whilst admitting that the secretion proceeds from the large cells, maintains that they do not entirely break down, but merely yield up their contents, their nuclei and the protoplasm surrounding the nuclei remaining to repair the loss.‡

To recapitulate—the several conditions under which a flow of saliva may be made to occur, are—1. By the reflex action of the medulla oblongata, the submaxillary and otic ganglia, excited by impressions conveyed through the glosso-pharyngeal and gustatory of the fifth, and taking effect through the motor branches of the facial, running in the chorda tympani and auriculo-temporal nerves. 2. By calling into play the muscles of mastication, the effect being probably due to coincident excitation of the nerves supplying the glands with those distributed to the muscles. 3. By mental stimuli, as by the sight or thought of sapid food. 4. By poisons circulating in the blood, as Camphor, Curare in small doses, Physostigmin, Pilocarpin, the Calabar bean, Chloroform, and the Salts of Mercury. 5. By lesion of certain parts of the encephalon, as the floor of the fourth ventricle, and the cortical substance of the hemispheres near the *sulcus cruciatus*;§ by stimulation of the upper extremities of the sympathetic or pneumogastric nerves divided in the neck, or of the central extremity of the divided sciatic or any other afferent nerve,‖ which is not due (entirely at least) to the effects of this irritation in producing increase of blood pressure. If the stimulation of the sciatic be continued for more than a minute or two, an inhibitory influence is excited on the secretion.¶ The chorda tympani appears to contain fibres exciting an inhibitory action on the blood-vessels, as well as motor fibres inducing secretion. For it has been shown by Heidenhain and Kenchel that after the administration of atropin or daturin, if the chorda tympani be stimulated, the vessels dilate, permitting a freer current of blood through the gland, although there is no increase in the amount of saliva secreted. The submaxillary gland responds much more readily to the electric stimulation of its secreto-motor nerves than the parotid.** 6. By nausea.

109. On its entrance into the Stomach, the food is subjected to the operation of the *Gastric Juice*, which is secreted by the follicles in its walls, or by a certain part of them. This follicular apparatus is extremely extensive, and

Nüssbaum may have excised small portions of the parotid gland, which is very active in effecting the conversion of starch into sugar. Both Grützner and Nüssbaum find that the cells of Acini are only slightly, whilst those lining the duct are intensely blackened with osmic acid.

* "Studien des Physiol. Inst. zu Breslau," 1868, p. 1.

† Notes to the French translation of Frey's "Histology," p. 439, quoted in Küss, "Physiologie," 1873, p. 265.

‡ See also for a similar view, Ewald, "Centralblatt," 1870, p. 375.

§ Landois, "Lehrbuch der Physiologie," 1879, p. 269.

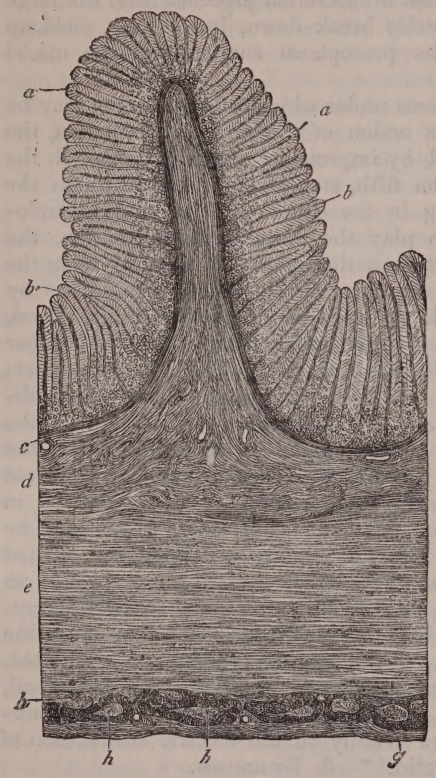
‖ See P. Grützner, Pflüger's "Archiv," Band vii. 1873, p. 522; see also Owsiannikow Tschiriew. Heidenhain has shown that the fibres of the chorda tympani nerve exciting the submaxillary gland to increased secretion, are distinct from the inhibitory vaso-motor fibres, since the administration of atropin paralyzes the former, but leaves the latter functionally intact.

¶ Pawlow, Pflüger's "Archiv," 1878, p. 277.

** Bernard, "Leçons de Physiologie Opératoire," 1879, p. 535.

makes up the chief part of the thickness of the gastric mucous membrane. The matrix of the mucous membrane of the stomach in which the glands are imbedded consists of adenoid tissue, or a fibrous network containing cells and nuclei. This is more dense in some parts than in others, which has led various observers to admit the existence of lenticular or solitary glands in the region; but these spots differ from the lenticular glands, in being destitute of a limiting membrane.* The interior surface of the stomach, thrown by contraction when the viscus is empty into irregular folds or rugæ (Fig. 70, A), presents throughout the greater part of its extent, and especially near the Pylorus, small vascular processes or prolongations of the mucous membrane (B),† resembling the villi of the small intestine, of which they must be considered as the rudimentary condition, but differing essentially from them in the circumstance that they contain no lacteal vessels. If the mucous membrane be divided by a section perpendicular to the surface, it is seen to be almost entirely composed of a multitude of parallel tubuli closely applied to each other, their cæcal extremities abutting against the muscularis mucosæ, and their open ends being directed towards the cavity of the Stomach. Between the tubuli, blood-vessels pass up from the submucous tissue, and form a vascular network on its surface, in the interspaces of which the orifices of the tubes are seen.

Fig. 69.



Transverse section through the *fundus of the stomach* in a child.—*a*, *a*, columnar epithelium: *b*, *b*, peptic gland tubes: *c*, muscularis mucosæ, about 1-250th of an inch in thickness, chiefly composed of longitudinal fibres: *d*, submucous tissue; *e*, circular muscular layer; *g*, peritoneum; *h*, ganglia of Auerbach.

The *Septa* contain the blood-vessels (*a*, *a*), and form polygonal meshes around the tubuli. They project some distance beyond the orifices of the tubes into the cavity of the stomach, and form the prominent folds or "plicæ villosæ," which, when the membrane is inspected with the naked eye, or with a lens of low power, give to it its trellis-like aspect.

These tubular glands, the number of which is estimated by Sappey at nearly five millions,‡ do not everywhere present the same structure. Krause,§ who has described the glands with great care, distinguishes simple and compound gastric glands and pyloric glands. In each of the *simple glands* he dis-

* See Klein, *op. cit.*, 548.

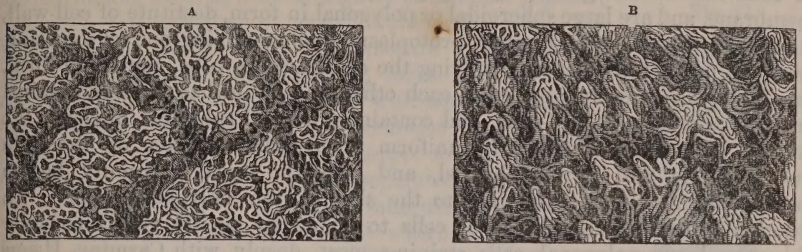
† This fact was first brought into prominent notice by Dr. Niell, in his Memoir 'On the Structure of the Mucous Membrane of the Human Stomach,' in the "Amer. Journ. of Med. Sci.," Jan. 1851.

‡ Sappey, "Traité d'Anatomie," t. iv., 1873, p. 183.

§ "Allgemeine Anatomie," 1876, p. 206.

tinguishes four parts—the mouth, the neck, the body, and the cæcal extremity. The mouth, the length of which is about one-fourth of that

FIG. 70.



Appearance of the lining membrane of the *Stomach*, in an injected preparation.—A, from the convex surface of the rugæ; B, from the neighbourhood of the pylorus, where the orifices of the gastric follicles occupy the interspaces of the deepest portions of the vascular network.

of the whole tube, is surrounded by the projecting folds or plicæ already referred to, and is lined by a simple layer of columnar epithelium similar to

FIG. 71.

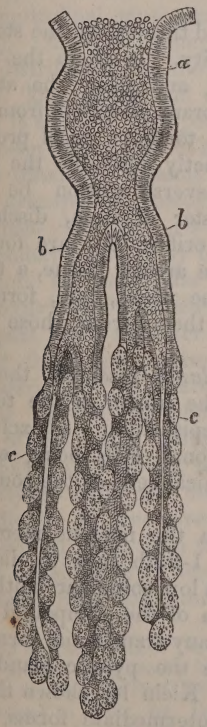


FIG. 72.

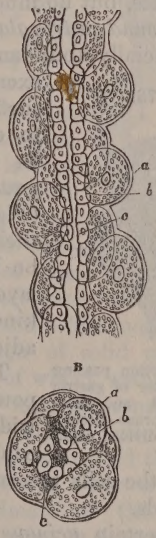


FIG. 71. *Compound gastric gland.*—*a*, common trunk; *b*, *b*, its chief branches; *c*, *c*, terminal cæca with spheroidal gland-cells.

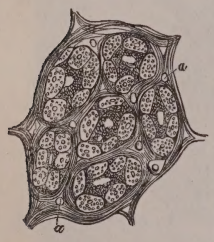
FIG. 72. Portions of one of the compound gastric glands highly magnified, as seen longitudinally (A), and in transverse section (B).—*a*, basement membrane; *b*, large glandular delomorphous cells; *c*, small adelomorphous cells surrounding the cavity.

that investing the plicæ, with a few interspersed goblet-cells. The oval nuclei of these cells are situated near their attached ends, and between these extremities are found small protoplasmic masses destined to supply the place of detached or disintegrated cells. The *neck*, which succeeds, is narrower and not so long as the mouth. It is narrower also than

the body. In it the cylindrical cells become successively shorter, till they assume an almost polygonal form. A few conical cells lie in the axis of the tube at this part. In the *body* and *cæcal extremity* two very distinct forms of cells can be recognized: the peptic cells, which are in contact with the membrane, and are large spheroidal or polygonal in form, destitute of cell-wall,* colourless, with darkly granular protoplasm, and containing one or sometimes two oval nuclei; the other occupying the centre of the tube, conical in form,† smaller in size, closely applied to each other, and somewhat indistinct, faintly granular, destitute of cell-wall, and containing a small spherical nucleus. The conical cells form a tolerably uniform layer near the axis of the tube, but some lie free in the channel, and near the cæcal extremity become rather larger, almost attaining to the size of the polygonal cells. The reaction of the different kinds of cells to colouring agents varies considerably, the large polygonal cells staining most deeply with Carmine, Hæmatoxylin, Anilin, and Potassic bichromate, whilst the ordinary columnar cells are less deeply tinged, and the conical cells least of all. The protoplasm of the polygonal cells clears up on the addition of 0·5 to 5 per cent. solution of acetic, or ·002 to ·005 of nitric acid, whilst that of the conical cells becomes more cloudy. It then, however, takes anilin blue, becoming more deeply tinged during fasting than in hunger. Both kinds contain various albuminous bodies, but no mucin.

The *compound gastric glands* (Fig. 71) are scattered throughout the stomach, but are especially abundant in the cardiac extremity. In these the simple excretory duct soon widens, and near the attached surface of the mucous membrane gives off from three to eight cylindrical slightly tortuous cæcal processes. In other respects they exactly resemble the simple gastric glands. If a transverse section be made (Fig. 73) through a cluster of cæca, discharging their contents by a single orifice, they are found to be held together by delicate areolar tissue, a thicker layer of which surrounds the whole, and, forming a kind of septum, isolates them from those of the adjoining glands.

Fig. 73.



Transverse section passing through a cluster of gastric cæca, separated and surrounded by fibrous tissue; *a*, *a*, orifices of divided capillaries.

The *pyloric* or *mucous glands* resemble the compound gastric glands, but the lumen of the tubes is wider, and although the epithelium is exclusively columnar, conical or polygonal cells being entirely absent, yet the cells present the reactions of the conical cells of the compound gastric glands.

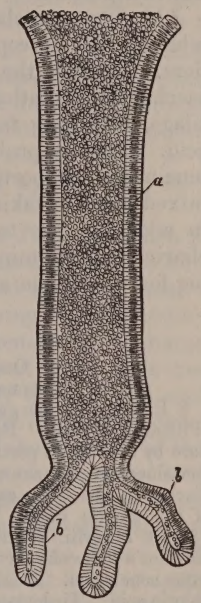
Lastly, certain *acinous* glands are contained in the mucous membrane. These are round or oval bodies about 1-50th to 1-25th inch in diameter. They project into the submucosa, and are lined by a low columnar epithelium. They may be regarded as a more complicated form of the compound gastric or pyloric glands, between which and themselves many transitional forms may be found. At the free border of the pyloric valve the pyloric glands cease suddenly, and are replaced by the acinous glands. Klein has shown that the several forms of glands are connected by so many intermediate forms, that it is impossible to draw a very definite line between those secreting mucus

* Labzellen, Heidenhain's "Belegzellen;" Rollet's "delomorphous cells;" Juke's "polygonal cells." ("Centralblatt, f. d. Med. Wiss," 1872, No. 47.)

† Heidenhain's "Hauptzellen;" Rollet's "adelomorphous (ἄδηλος, unapparent; μορφή, form) cells."

exclusively, and those which produce both pepsin and mucus.* According to M. Cl. Bernard,† when the stomach is empty, the columnar-epithelium which lines the neck of the glands completely blocks-up their orifices, so that during fasting these appear as slightly prominent papillæ; but when the secretion of gastric fluid commences, this epithelium is cast-forth by the pressure from beneath. The *lymphatics* of the stomach‡ form two layers, a superficial and close network, often with sinus-like dilatations, surrounding the cæcal extremities of the peptic glands, and a deeper layer with larger meshes lying in the submucous areolar tissue, and separated from the first by the thin stratum of unstriated muscular fibre, known as the *muscularis mucosæ*, through which many vessels connecting the two strata pass. The *nerves* of the stomach are derived from the pneumogastrics, or rather from the branch of the spinal accessory on each side that joins the pneumogastric, and from the solar plexus of the great sympathetic. They are divided into two layers; one of which forms a plexus in the submucous tissue (Meissner's plexus), whilst the other lies amongst the fasciculi of the longitudinal muscular coat (Auerbach's plexus; Fig. 69, *h*). In the former, ganglia are somewhat sparingly distributed; in the latter, they are abundant.§

Fig. 74.



Pyloric gland, with cylinder-epithelium.—*a*, wide trunk; *b*, *b*, its cæcal appendages.

110. The nature and composition of the *Gastric Juice* which is secreted and poured forth by the peptic follicles have been the subject of much discussion among Chemists. When obtained without admixture with saliva, it is a clear, transparent, colourless or slightly-yellow fluid with very little viscidity. Its sp. gr. is 1·001 to 1·010. It is not rendered cloudy by being boiled. Microscopic examination indicates the persistence of a few of the cells exuviated from the interior of the gastric follicles; but these for the most part leave no other traces than their nuclei and a fine molecular matter arising from their disintegration. The proportion of solid matter which the Gastric Juice contains is about 0·5 per cent., of which rather more than half is organic substances, and less than half mineral constituents, the chief of the latter being sodium, potassium and calcium chloride, and the phosphates of calcium, magnesium and iron. It is estimated that the total quantity secreted per diem is about one-tenth of the body weight; but it is difficult to give even an approximative estimate of the quantity of fluid poured forth from the walls of the stomach, since it is certain that it varies considerably, according to the nature of the substances ingested. Corvisart, from experiments on dogs,‖ estimated it at about 1-20th of the

* The best accounts of the structure of the mucous membrane of the stomach, and of the gastric glands, are given by Messrs. Todd and Bowman, "Physiological Anatomy," vol. ii. pp. 190 *et seq.*; by Prof. Kölliker, "Mikros. Anat.," Band ii. § 163; by Henle, "Eingeweidelehre," p. 152; by Dr. Klein, Stricker's "Histology," 1870, p. 543: Krause, "Allgemeine Anatomie," 1876; and by Sappey, "Traité d'Anatomie Descriptive," vol. iv.

† "Gaz. Méd.," Mars, 1844.

‡ Teichmann, "Das Saugader System," 1861, p. 76; Lovén, quoted in "Quain's Anatomy," p. 356, "Om lymfvägarna i magsäckens slemhinna. Nord. Med. Arch.," 1873; also H. Watney, "Centralblatt, f. d. Med. Wiss.," 1874. No. 48.

§ For the mode of termination of the nerves in the stomach of the Frog, see K. Trütschel, "Centralblatt," 1870, p. 115.

‖ Longet, "Physiologie," 1860, vol. i. p. 183.

weight of the animal per diem; Harley,* at 1-15th; Lehmann, at 1-10th; whilst Gruenewaldt† obtained nearly $\frac{3}{4}$ lb. avoird. from a woman of 116 lbs. weight, with a gastric fistula, in fifteen minutes; and Schmidt‡ gives as the mean of experiments on the same woman, about 9000 grains hourly during active digestion.

111. The most characteristic feature of the Gastric Juice is its decided *acidity*, which is very perceptible to the taste, and is constant throughout the animal kingdom. In man, the acidity of the juice when secreted under the influence of mechanical irritation, or of some not very readily soluble substance, as cartilage, after long fasting, is invariably due to the presence of hydrochloric acid. This is probably in combination with some feeble base as glycocol or leucin, the proportion being 0·2 per 1000, but when digestion of ordinary mixed food is taking place, lactic, butyric, and acetic acids may be found in addition, due to the fermentation and decomposition of fats, milk, saccharine and albuminous compounds. Even in the pure gastric juice after standing for some time an organic acid, presumably sarcolactic acid, is developed.§

* "Medico-Chirurgical Review," 1860, p. 211.

† Quoted by M. Edwards, "Leçons," t. vii. 1862, p. 24.

‡ "Annal. der Chemie," von Liebig und Wöhler, vol. xcii. p. 42.

§ Richet, "Du suc gastrique," in "Journal de l'Anatomie," 1878, p. 278, *et seq.* Heidenhain (Pflüger's "Archiv," Band xix. 1879, p. 148) obtained the gastric secretion of the dog nearly pure by isolating a portion of the fundus of the stomach, and found that in that animal it contained on an average as much as 5·2 parts per 1000 of hydrochloric acid. Much discussion has been carried on amongst chemists in regard to the nature of the acid of the gastric juice. The experiments of Berzelius ("Annal. d. Chemie. et de Phys.," 1813, t. lxxxviii.) seemed to show that the acid might be lactic; and Chevreul (see Milne-Edward's "Leçons sur la Physiol.," t. vii. p. 25) and Leuret and Lassaigne arrived at the same conclusion. Prout ("Phil. Trans.," 1825), however, early maintained that it was hydrochloric acid. Tiedemann and Gmelin ("Traité de la Digestion," 1826) thought it was acetic acid. Frerichs (Wagner's "Handwörterbuch," t. iii. p. 780) that it was butyric; and Blondlot ("Traité Anat. de la Digest." 1841, p. 214) that it was the acid calcium-phosphate. Even recent experiments are contradictory. M. Rabuteau ("Bullet. de la Soc. de Biol.," 1874, pp. 96 and 400; see also Tardieu and Roussin, "Les Empoisonnements;" and Dragendorf, "Manuel de Toxicol.," 1874, p. 486) treated gastric juice with quinine, and then extracted the salt of quinine thus formed with amylic alcohol. Under these circumstances the salt obtained was always the hydrochlorate, and not the lactate of quinine. M. Laborde ("Mem. de la Soc. de Biol.," 1874, p. 63, and "Gaz. Med. de Paris," 1874, No. 9) on the other hand has shown that water acidulated with 3 parts in 1000 of hydrochloric acid is capable of converting starch into sugar when the mixture is heated to 150° C, under a pressure of five atmospheres; but the gastric juice is incapable of effecting this change under the same circumstances. Reoch ("Journ. of Anat. and Phys.," vol. xiv. p. 274) admits the presence of hydrochloric acid with traces of lactic acid, on the ground that potassium sulphocyanide, mixed with citrate of iron and quinine, changes colour on admixture with gastric juice, owing to the formation of iron sulphocyanide, a change which is induced by mineral, but never by organic acids. Szabó ("Zeits. f. Phys. Chemie.," 1877, p. 140) finds that both acids are often coincidently present, but that in dyspepsia hydrochloric acid is absent. The latest observer, C. Richet ("Journ. de l'Anat, et de la Physiol." Année xiv., 1878, p. 213) adopting a special method of procedure, suggested by Berthelot, in which ether is employed as a vehicle to abstract the acid from the juice, arrives at the conclusion that there is only one acid, and that one containing cholorin, and therefore probably hydrochloric in combination with some feeble base as leucin or glycocol, no lactic acid being demonstrable, though there may be a trace of sarcolactic acid. That the acidity of the gastric juice is attributable to lactic acid has been maintained by Huhnefeld (Valentin's "Repert für Anat. Phys.," 1841, p. 287), Thomson ("Lond., Edin. and Dublin Phil. Mag." 1841), Lassaigne ("Journal de Chem. Med.," 1844, p. 183), Lehmann ("Ber. d. Gesells. der Wissenschaften," Leipzig, 1847), Heintz (W. Heintz "Pharm. Chem. Centralblatt," 1849, and "Jenaische Ann. für Phys. Med.," 1849, p. 222), Claude Bernard ("Lec. d. Phys. exper. appliquée à la Méd.," t. ii., 1856), Laborde ("Nouvelles Recherches de Gaz. Méd. de Paris," 1874, No. 32–34), and Dionys Szabó (Szabó, "Zeits. f. Physiol. Chemie.," Band i., 1877–78, p. 140). This last-named experimenter adopted several modes of procedure, the more important of which were those suggested by

Dr. F. G. Smith,* on examining the contents of the stomach of Alexis St. Martin, two and a half hours after a small quantity of bread had been eaten, obtained evidence of the presence of lactic, and of the absence of all but the slightest trace of hydrochloric acid. To explain the discrepant results obtained by various observers, allowance must be made for differences existing in different animals, and perhaps also at different ages, since M. Wasmann† has remarked that the pepsin of the stomach of the pig is entirely destitute of the power of coagulating milk, although the pepsin of the stomach of the calf possesses it in a very high degree; from which he is led to suppose that the power of the latter depends upon a particular modification of pepsin, or perhaps upon another substance accompanying it, which ceases to be formed when the young animal is no longer nourished by the milk of its mother (see p. 70, vi.).

112. The peculiar organic constituent of the Gastric Juice, to which the name of *Pepsin* (p. 69) has been given, is not an albuminous substance but a hydrolytic ferment, and appears to be secreted and stored up in the small or adelomorphous cells of the stomach in a neutral state during the intervals of digestion, and to be only mingled with the acid at the moment of discharge.‡ At the commencement of the digestive process the small cells have been observed to swell and to become transparent, and they then contain much pepsin, but in the later stages of digestion they shrink and present a cloudy aspect, and at this period have a much smaller amount of the ferment in their interior. It is probable that whilst chiefly formed in the smaller cells of the peptic glands a small quantity of pepsin is secreted also by the mucous glands;§ but no appearances have been observed favouring the idea that the small cells undergo conversion into the larger delomorphous cells. If the stomach of an animal be thoroughly washed with water till all trace of acidity is removed, a fresh portion of pepsin, possessing a perfectly neutral reaction, can be obtained on further maceration; and Bernard found that on injecting successively lactate of iron and ferrocyanide of potassium into the jugular vein of a rabbit, no blue discoloration of the blood, secretions or tissues generally was observable on account of their alkaline reaction, though this could be immediately produced by the addition of sulphuric or other acid. On examining the stomach, however, he found that whilst the gastric follicles were free from colour, the surface of the mucous membrane was uniformly tinted. From these experiments, the inference may be fairly drawn that whilst the pepsin of the gastric juice is secreted by the cells lining the gastric follicles, the acid is formed, or at least excreted, by the most superficial

Rabuteau and by Baumann. Rabuteau's method of determining whether lactic or hydrochloric acid is present in a fluid, consists in mixing a solution of potassium iodate with the starch paste, and adding a little potassium iodide. If this fluid contain free hydrochloric acid iodin is set free, and the starch is tinted blue; lactic acid, however, in the proportion of 1·1000 sets no iodin free, and consequently causes no change of colour. Baumann's method consists in adding potassium phenyl-sulphate to the fluid or juice. If hydrochloric acid be present, Phenol is given off on distillation, which is easily recognised by a solution of bromin. Lactic acid in the proportion of 1·1000 causes no such decomposition. There are cases indeed perhaps occurring in dyspeptics, in which the gastric juice contains no hydrochloric, but only lactic acid. And, on the other hand, in some instances the gastric juice contains only hydrochloric acid.

* "Experiments upon Digestion," Philadelphia, 1856.

† See Prof. Graham's "Elements of Chemistry," pp. 1031-1033.

‡ See Bernard, "Leçons," 1859, p. 376; and Schiff, "Physiologie de la Digestion," 1868, Leçons 21-24.

§ See Ebstein, Pflüger's "Archiv," Band viii. p.122, and Grützner, idem. Band xvi. p.105.

cellular layers of the mucous membrane.* The quantity of pepsin that is discharged from the body is probably very small, reabsorption taking place as it traverses the alimentary canal.† It is found in nearly all the muscles and in the blood of the pig, but only traces can be found in the urine of that animal. If the whole of the gastric juice be allowed to drain away through a gastric fistula, the urine becomes alkaline in consequence of the absorption of the alkaline fluids of the intestine.

113. All the more recent and accurate experiments of those who have studied the chemistry of digestion lead to the conclusion that the solvent powers of gastric juice are chiefly exerted upon albuminous compounds, and that its action is comparatively slight upon farinaceous, saccharine and oleaginous substances. Peptic digestion is essentially an acid digestion or a digestion of solution, and it seems to stand in the place of a high temperature and a powerful oxidizing agent. When an albuminous substance, such as white of egg, fibrin, or casein, is exposed to the action of the gastric juice, it swells up, softens and dissolves, becoming converted into some modification of a substance termed *peptone;* this, though varying with the form of albumin from which it is derived, differs from albumin in being no longer precipitable from its neutral solution by any change in the reaction, and in having acquired the power of passing through an animal membrane. It has been ascertained that peptones are capable of maintaining life,‡ and there is evidence to show that soon after entering the blood they are reconverted into albumin; the object of the change of the colloidal albumin into the crystalloid as peptone being to facilitate the entry of the albuminous compounds into the blood. In the subjoined note the principal features of the peptones are given.

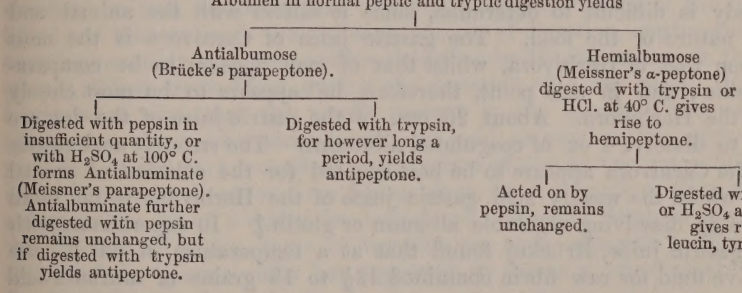
Peptones.—The term peptones is applied to the substances that immediately result from the action of hydrochloric and sulphuric acids, of trypsin or of gastric juice, on albuminous compounds. In order to prepare one form, Hofmann ("Lehrbuch der Zoochemie, 1878, p. 332) recommends fresh, finely-divided fibrin to be macerated with five or six times its volume of dilute hydrochloric acid (containing two parts in 1000). As soon as the fibrin has become gelatinous a little pepsin dissolved in glycerin is poured over it, and it is kept in a water bath, at a temperature of 50°—60° C. (122°—140° F.). Large bubbles form, and in the course of a few hours an opalescent solution is obtained, in which a few fibrinous flocculi float. This is strained and neutralized with sodium-carbonate, so that blue litmus-paper is feebly tinted of a violet colour. The precipitate is allowed to settle, and the fluid is filtered, slightly acidified, heated, and again filtered. Peptone is then thrown down by absolute alcohol, and all fat removed from it by washing with alcohol and ether. It is now macerated for two or three weeks in absolute alcohol to remove the last traces of unchanged albumin. The white mass, freed from alcohol, is dissolved in a little warm water, precipitated by absolute alcohol, and the precipitate is finally dried *in vacuo* at a temp. of 30° C. (86° F.). Fresh peptone thus obtained is a white curd-like substance, which, whilst still moist, changes at a temp. of 80°—90° C. (177°—194° F.) to a yellowish fluid, resembling melted fat, which hardens on cooling. Dry peptone is a yellowish-white, transparent, amorphous, friable, hygroscopic substance, soluble in water, especially if slightly warmed, the solution possessing levo-rotatory power on a ray of polarised light. If long kept, or if it has been dried over 30° C. (86° F.) it dissolves with more difficulty. Though insoluble in absolute alcohol it dissolves in spirit of wine, in proportion to the amount of water present in the fluid. The watery solution is neutral, has a levo-rotatory power, and diffuses easily through all animal and vegetable

* Schiff considers that, as in the case of the Pancreas, a kind of "charging" of the glandular follicles occurs during the intervals of digestion, the pepsin being derived from certain peptogenic materials in the blood supplied by the previous digestion of albuminous compounds, or of dextrin. This view is strongly opposed by Fick ("Verhand. d. phys. med. Gesells.," N.F., Band ii. 53), who found that the stomach of a dog secreted active gastric juice fifteen hours after the last full meal, and that in rabbits, fasting did not diminish the digestive activity of the stomach, whilst the ingestion of dextrin did not augment it.

† Brücke, "Vorlesungen," p. 295; Schiff, op. cit., vol. ii., "Leçon," xxi.

‡ Plósz, Pflüger's "Archiv," Band ix. p. 325.

membranes, in which respects it stands in strong contrast to all the albumins, from which it further differs in not undergoing coagulation at 100° C. (212° F.) and in the precipitate which is thrown down in its solution by concentrated nitric acid, aceto-ferrocyanide of potassium and neutral alkaline salts being redissolved on the application of a gentle heat. They are precipitated by both acetates of lead, and from an acid solution by the biliary acids. They are also thrown down by tannic acid, potasso-mercuric iodide, basic acetate of lead, phosphor-wolframic and phosphor-molybdic acids. On the addition of a little sodium-hydrate to its solutions in water, and then of a drop or two of an extremely dilute solution of copper-sulphate, a rose-red tint is produced (von Gorup-Besanez, "Biuretreaction"). On the addition of concentrated sulphuric acid to the solutions of both gastric and pancreatic peptones the liquid is coloured bluish-violet, with a green fluorescence, and an absorption band appears between *b* and *F*. Nitric acid disturbs this reaction, and the addition of salt makes it more distinct (Adamkiewicz's test). The statements just made in regard to fibrin-peptone hold good in all essential respects for the peptones obtained from other albumins. They all have a strong disposition to form salt-like combinations with very different neutrals. The composition of peptone from fibrin, according to Kossel,* is C 48·97, H 7·06, N 15·14, S 1·16.† *Parapepton* or A-pepton, *Dyspepton* or B-pepton and *Metapepton*, or C-pepton are peptones obtained by Meissner, of which the first is precipitated by nitric acid and by potassium ferrocyanide, the second by potassium ferrocyanide alone, and the third by neither of these reagents. According to Brücke, metapepton is composed of two substances, *hydrophyr*, which is soluble in water, and *alkophyr*, which is soluble both in water and in alcohol. Leucin and tyrosin are amongst the terminal products of gastric digestion. Kühne's (Verhand, "Nat. Hist. Med. Ver." Heidelb., 1876) view of the disintegration of proteids under the action of the digestive fluids may be understood from an inspection of the accompanying scheme :—


Albumen in normal peptic and tryptic digestion yields
Antialbumose (Brücke's parapeptone).
Hemialbumose (Meissner's α-peptone) digested with trypsin or HCl. at 40° C. gives rise to hemipeptone.
Digested with pepsin in insufficient quantity, or with H_2SO_4 at 100° C. forms Antialbuminate (Meissner's parapeptone). Antialbuminate further digested with pepsin remains unchanged, but if digested with trypsin yields antipeptone.
Digested with trypsin, for however long a period, yields antipeptone.
Acted on by pepsin, remains unchanged.
Digested with trypsin, or H_2SO_4 at 100° C., gives rise to leucin, tyrosin, &c.

It must not be supposed that the whole of the albuminous compounds introduced into the stomach under ordinary circumstances are converted into peptone. Some forms of albumin, as white of egg, undergo, in part, direct absorption, whilst a part is absorbed as soon as it is converted into syntonin (Brücke). This action of the gastric solvent upon the azotized constituents of the food is dependent upon several accessory conditions. One of the most important of these is *temperature*. A heat of from 96° to 100° is required to keep up the solvent process, which is retarded according to the depression of the thermometer below this standard; so that at the ordinary temperature of the atmosphere it is completely suspended, to be renewed, however, with an increment of heat. On the other hand, a trifling elevation of temperature above 100° F. occasions a decompositon in the gastric juice, which entirely destroys its solvent power. The next condition, which specially affects the time required for the process of solution, is *motion*. This does not act mechanically, by way of "trituration," as was once supposed; for food is found to be digested, when enclosed in metallic balls perforated to admit the

* "Zeits. f. Phys. Chem.," Band iii. 1879, p. 58.

† See Rob. Herth in Hoppe-Seyler's "Zeits. f. Chemie.," 1877, Band i. p. 279. See also Adamkiewicz, "Virchow's Archiv.," Band lxxv., H. i., p. 114; Kossel "Centralblatt, f. d. Med. Wiss.," No. 1, 1877; Plósz, Pflüger's "Archiv," Band ix. p. 325; Kistiakowsky, idem., p. 438; Plósz, idem., Band x. p. 536; Maly, idem., p. 585; A. Henninger, "Comptes Rendus," lxxxvi. No. 22; Hofmeister, "Zeits. f. Physiol. Chemie," Band ii. 206.

access of gastric juice to their interior. But it answers the purpose of thoroughly subjecting the whole of the alimentary bolus to the agency of the gastric solvent, by bringing each part successively into contact with the lining membrane of the stomach, from the surface of which the fluid is effused. The *removal of the matters already reduced or dissolved*, also, has a most important effect in facilitating the solution of the remainder. This removal is due in part to the absorption of the matters in a state of solution, into the blood-vessels of the walls of the stomach; and in part to the successive escape of the reduced portions through the pyloric orifice. The importance of the previous state of *minute division* and *incorporation with aqueous fluid*, in promoting the action of the gastric solvent, has been already dwelt on (§ 101). The presence of either trypsin, bile or strong acids, or of alcohol, altogether arrests the solvent action of the gastric juice. A concentrated saline solution, or the employment of any mechanical means which prevent the swelling of albuminous substances materially interferes with gastric digestion. Gelatin and gelatin-yielding tissues, like tendon, fibrous tissue and skin, are only slowly acted on by the gastric juice, the fluid resulting from their solution retaining for some time its power of solidifying; ultimately, however, a syrupy fluid results, which will not gelatinize, and which will dialyze to some extent.* The solvent power of the gastric juice in the living body is difficult to determine, since it differs with the animal and with the nature of the food. The gastric juice of Carnivora is the most active, then that of Herbivora, whilst that of man appears to be comparatively feeble; and in this point, therefore, he appears to be most closely allied to the Herbivora. About 20 ozs. of the gastric juice of the dog are required to dissolve 1 oz. of coagulated albumin.† The strongly acid gastric juice of the Carnivora appears to be best adapted for the solution of animal albumin, whilst the weakly acid gastric juice of the Herbivora is far more efficacious in dissolving vegetable albumin or glutin.‡ In experiments with artificial gastric juice, Brücke§ found that at a temperature of 65° F., the most active fluid for raw fibrin contained 12½ to 15 grains of muriatic acid in one litre (1·76 pints), whilst the most active fluid for albumen, coagulated by heat, contained from 18·5 to 24·7 grains of this acid in the litre.

114. The presence of a *special ferment*, capable of *converting starch into sugar* in the fluids secreted by the stomach, is shown by the experiments of Dr. Smith on Alexis St. Martin, evidence of the presence of grape-sugar having been found an hour and a half after bread and water had been introduced through the fistulous orifice, the man carefully avoiding to swallow his saliva during that period. Under ordinary circumstances the conversion of starch into sugar is effected by the continuance of the action of the saliva with which the food has been impregnated in the mouth, or which has been subsequently swallowed. The action has been found to be materially checked when, by tying the œsophagus, the entrance of saliva into the stomach is prevented.‖ It has been noticed by Hoppe-Seyler, that when large quantities of cane-sugar are taken, a condition of gastric catarrh, attended with the secretion of much mucus, is induced, and that the cane-sugar then undergoes, probably in consequence of its rapid transformation into grape-sugar, speedy absorption. Oleaginous substances appear to be merely liquefied and finely

* See Henle and Meissner's "Bericht," 1860, p. 269; and Henle and Pfeuff's "Zeitschrift," Band xiv. 1863, p. 303; Mohlenfeld, Pflüger's "Archiv," 1872, Band v. p. 381; v. Wittich, idem., p. 435. † Lehmann and Corvisart.

‡ Koopman's "Nederland. Lancet," t. v. 1856. § Op. cit. p. 300.

‖ Brucke, "Vorlesungen über Physiologie," 1874, p. 300.

divided, in which state they are diffused through the pulpy chyme.* The decomposition of the fats into fatty acids and glycerin, sometimes commences in the stomach, as is indicated by the presence of the butyric acid which has been so frequently observed. The horny tissues of animals, as the nails, hair, and epidermis, elastic tissue, and mucin, are but slightly, if at all, acted on by the gastric juice.

115. It is only when either alimentary or some other substances capable of exciting irritation are present in the stomach, that the gastric juice is poured forth. So long as it is empty, the secretion which moistens its walls is neutral or even alkaline; but as soon as food is taken, acid is poured forth, and this in increasing quantities, until a certain time after the commencement of the digestive process, when the acidity of the stomach is at its maximum. In proportion as the alimentary matter is dissolved, however, and is either at once absorbed, or escapes through the pyloric orifice, the acidity of the stomach diminishes; and as soon as its cavity is emptied, the secretion of its walls is neutral again.† The circumstance that the stomach does not itself undergo digestion, even when that process is being actively performed on its contents, is of considerable interest, and must be attributed to the saturation of the whole mucous membrane with blood containing a large proportion of alkaline salts, for it has been shown by Dr. Pavy, that if one or two vessels of the stomach be tied, the parts thus deprived of the circulatiou of the blood are killed and then undergo the ordinary process of digestion, perforating ulcers occuring precisely analogous to those described by Hunter as seen in the bodies of men killed by accident during the digestion of a full meal. It must be remembered, also, that the pepsin present in the glands of the stomach is inoperative till it has mingled with the acid secreted on the surface. The mere fact of the part presented to the action of the gastric juice being alive does not prevent digestion from taking place, for if a snail, or slug, the leg of a frog, or the ear of a rabbit, be introduced through a fistulous opening into the stomach of a dog, signs of digestion are soon apparent.‡ The solvent action of the gastric juice has suggested its use as a remedial agent in old sores and fistulæ.

116. A very important series of observations on the conditions under which the gastric juice is secreted was made some years since by Dr. Beaumont, in the remarkable case of Alexis St. Martin, already several times referred to.§ "The inner coat of the stomach (as seen through the fistulous orifice), in its natural and healthy state, is of a light or pale pink colour, varying in its hues according to its full or empty state. It is of a soft or velvet-like appearance, and is constantly covered with a very thin, transparent viscid mucus, lining the whole interior of the organ. By applying aliment or other irritants to the internal coat of the stomach, and observing the effect through a magnifying glass, innumerable lucid points, and very fine papillæ can be seen arising from the villous membrane, and protruding through the mucous coat, from which distils a pure, limpid, colourless, slightly viscid fluid." (The papillæ here described appear to be the orifices of the gastric follicles, which are usually closed by their epithelial cells during fasting, and which would seem to become prominent when the *vis a tergo* of the secreted

* Frerichs in Wagner's "Handworterbuch," Band iii., Art. Verdauung.

† See Dr. Bence Jones, in the "Medical Times," June 14, 1852; and Dr. Marcet, "Journal of the Chemical Soc.," 1862.

‡ See Dalton, "Amer. Journ. Med. Sci.," April, 1865, p. 334.

§ See Dr. Beaumont's "Experiments and Observations on the Gastric Juice and the Physiology of Digestion," reprinted with Notes by Dr. Andrew Combe, Edinburgh, 1838.

fluid first causes this plug of cells to be cast forth.) "The fluid thus excited is invariably distinctly acid. The mucus of the stomach is less fluid, more viscid or albuminous, semi-opaque, sometimes a little saltish, and does not possess the slightest character of acidity. The gastric fluid never appears to be accumulated in the cavity of the stomach while fasting; and is seldom, if ever, discharged from its proper secerning vessels, except when excited by the natural stimulus of aliment, mechanical irritation of tubes, or other excitants. When aliment is received, the juice is given out in exact proportion to its requirements for solution, except when more food has been taken than is necessary for the wants of the system." The observations of Dr. Beaumont have been confirmed by those of M. Blondlot* and of M. Cl. Bernard,† which were made upon dogs in whose stomachs fistulous openings were maintained for a length of time. They found that the flow of gastric fluid is more excited by pepper, salt, and soluble stimulants, than it is by mechanical irritation; and that if mechanical irritation be carried beyond certain limits, so as to produce pain, the secretion, instead of being more abundant, diminishes or ceases entirely; whilst a ropy mucus is poured-out instead, and the movements of the stomach are considerably increased. The animal at the same time appears ill-at-ease, is agitated, has nausea, and, if the irritation be continued, actual vomiting; and bile has been observed to flow into the stomach, and escape by the fistulous opening. Similar disorders of the functions of the stomach result from violent pain in other parts of the body; the process of digestion in such cases being suspended, and sometimes vomiting excited. When acidulated substances, as food rendered acid by the addition of a little vinegar, were introduced into the stomach, the quantity of gastric fluid poured-out was much smaller, and the digestive process consequently slower, than when similar food, rendered alkaline by a weak solution of carbonate of soda, was introduced. If, however, instead of a weak solution, carbonate of soda in crystal or in powder was introduced into the stomach, a large quantity of mucus and bile, instead of gastric fluid, flowed into the stomach, and vomiting and purging very often followed. When very cold water, or small pieces of ice, were introduced into the stomach, the mucous membrane was at first rendered very pallid; but soon a kind of reaction followed, the membrane became turgid with blood, and a large quantity of gastric fluid was secreted. If, however, too much ice was employed, the animal appeared ill, and shivered; and digestion, instead of being rendered more active, was retarded. Moderate heat, applied to the mucus surface of the stomach, appeared to have no particular action on digestion; but a high degree of heat produced most serious consequences. Thus, the introduction of a little boiling water threw the animal at once into a kind of adynamic state, which was followed by death in three or four hours; the mucous membrane of the stomach was found red and swollen, whilst an abundant exudation of blackish blood had taken place into the cavity of the organ. Similar injurious effects resulted, in a greater or less degree, from the introduction of other irritants, such as nitrate of silver or ammonia; the digestive functions being at once abolished, and the mucous surface of the organ rendered highly sensitive. Amongst the most active stimulants of the gastric secretion is the saliva.

117. That the quantity of the Gastric Juice secreted from the walls of the stomach depends rather upon the general requirements of the system than upon the quantity of food introduced into the digestive cavity, is a principle of the highest practical importance, and cannot be too steadily kept

* "Traité Analytique de la Digestion."

† "Archiv. d'Anat. Gén. et de Physiol.," Jan. 1846.

in view in Dietetics. A *definite proportion* only of aliment can be perfectly digested in a given quantity of the fluid, unless the products of the action of the juice are removed, in which case the action of the pepsin may be regarded as continuous, the action of which, like other chemical operations, ceases after having been exercised on a fixed and definite amount of matter. The cessation of the action is due, however, not to the pepsin losing its solvent power, since a comparatively *minute proportion, as in the case of other ferments, will convert an almost indefinite quantity of albumin or fibrin into peptone*, but rather to the presence of a great excess of the dissolved peptone interfering with further action, just as the presence of alcohol or lactic acid in large quantity interferes with those processes of fermentation in which these substances are respectively formed; in accordance with this, it is found that when the gastric juice is saturated with peptone and ceases to digest, the addition of a little diluted acid will immediately enable it to effect the conversion of a fresh portion of albumen.* Nevertheless, the statement of Dr. Beaumont is perfectly true as regards the living subject, that "When the juice has become saturated, it refuses to dissolve more; and, if an excess of food has been taken, the residue remains in the stomach, or passes into the bowels in a crude state, and becomes a source of nervous irritation, pain and disease, for a long time." The unfavourable effect of an undue burthen of food upon the Stomach itself interferes with its healthy action; and thus the quantity really appropriate is not dissolved. The febrile disturbance is thus increased; and the mucous membrane of the stomach exhibits evident indications of its morbid condition. The description of these indications given by Dr. Beaumont, is peculiarly graphic, as well as hygienically important. "In disease or partial derangement of the healthy function, the mucous membrane presents various and essentially different appearances. In febrile conditions of the system, occasioned by whatever cause—obstructed perspiration, undue excitement by stimulating liquors, overloading the stomach with food, fear, anger, or whatever depresses or disturbs the nervous system—the villous coat becomes sometimes red and dry, at other times pale and moist, and loses its smooth and healthy appearance; the secretions become vitiated, greatly diminished, or even suppressed; the coat of mucus scarcely perceptible, the follicles flat and flaccid, with secretions insufficient to prevent the papillæ from irritation. There are sometimes found, on the internal coat of the stomach, eruptions of deep-red pimples, not numerous, but distributed here and there upon the villous membrane, rising above the surface of the mucous coat. These are at first sharp-pointed and red, but frequently become filled with white purulent matter. At other times irregular circumscribed red patches, varying in size and extent from half an inch to an inch and a half in circumference are found on the internal coat. These appear to be the effects of congestion in the minute blood-vessels of the stomach. There are also seen at times small aphthous crusts in connection with these red patches. Abrasion of the lining membrane, like the rolling-up of the mucous coat into small shreds or strings, leaving the papillæ bare for an indefinite space, is not an uncommon appearance. These diseased appearances when very slight do not always affect essentially the gastric apparatus. When considerable, and particularly when there are corresponding symptoms of disease—as dryness of

* In a paper on this subject ("Cenno sulle Ricerche fatte del Prof. Schiff," &c., abstract in "Centralblatt," 1872, p. 788), Schiff states that the stomach of a healthy dog in good physiological condition requires 200 litres (about 44 gallons) of water to develope its full digestive power, and the infusion of the stomach of a large dog in this quantity of water will digest 162 lbs. of albumen! Bennett ("Text Book of Physiology," 1872, p. 203) observes that one part of pepsin dissolved in 60,000 parts of water still possesses a distinct digestive action. See also Arthur Ransome, "Journ. of Anat. and Phys.," 1875-6, vol. 10, p. 459

the mouth, thirst, accelerated pulse, &c.—*no gastric juice can be extracted by the alimentary stimulus.* Drinks are immediately absorbed or otherwise disposed of; but food taken in this condition of the stomach remains undigested for twenty-four or forty-eight hours, or more, increasing the derangement of the alimentary canal, and aggravating the general symptoms of disease. After excessive eating or drinking, chymification is retarded; and, though the appetite be not always impaired at first, the fluids become acrid and sharp, excoriating the edges of the aperture, and almost invariably producing aphthous patches and the other indications of a diseased state of the internal membrane. Vitiated bile is also found in the stomach under these circumstances, and flocculi of mucus are more abundant than in health. Whenever this morbid condition of the stomach occurs, with the usual accompanying symptoms of disease, there is generally a corresponding appearance of the tongue. When a healthy state of the stomach is restored, the tongue invariably becomes clean.* According to the experiments of Dr. Severé,† the process of alcoholic fermentation is materially interfered with by fresh gastric juice, the obstructing agency being exerted upon the ferment, and not upon the fermentable substance. The lactic acid fermentation is not checked by fresh gastric juice; but this fluid, as Spallanzani long ago showed, is capable of completely stopping the progress of putrefactive fermentation. The Temperature of the stomach rises with the increase of vascular and secretory activity which takes place during digestion. Dr. F. Smith found the ordinary temperature of St. Martin's stomach while fasting to be 98°-99° Fahr., whilst during digestion it rose to 100°-101° Fahr.‡

118. That the secretion of Gastric Juice is affected in a very marked manner by conditions of the Nervous system is indicated by the effect of mental emotions in putting an immediate stop to the digestive process, when it is going-on with full vigour. It does not appear to be exactly determined by what channel such influence is conveyed. Experiments which have been made upon animals with a view of ascertaining the share which the nervous influence conveyed by the *Pneumogastrics* takes in digestion, have led to different, though perhaps when all the conditions are considered, to reconcilable results in the hands of different experimenters. The *immediate* result of the division of these nerves is to arrest the movements and the secretion of the stomach. The organ becomes pale and flaccid,§ the reaction of the juice feebly acid or neutral, and the quantity of pepsin produced diminished.‖ Any food that

* Dr. A. Combe's commentary on the above passage is too apposite to be omitted. "Many persons who obviously live too freely, protest against the fact, because they feel no immediate inconvenience, either from the quantity of food, or the stimulants in which they habitually indulge; or, in other words, because they experience no pain, sickness, or headache,—nothing, perhaps, except slight fulness and oppression, which soon go off. Observation extended over a sufficient length of time, however, shows that the conclusion drawn is entirely fallacious, and that the real amount of injury is not felt at the moment, merely because, for a wise purpose, Nature has deprived us of any consciousness of either the existence or the state of the stomach during health. In accordance with this, Dr. Beaumont's experiments prove, that extensive erythematic inflammation of the mucous coat of the stomach was of frequent occurrence in St. Martin after excesses in eating, and especially in drinking, even when no marked general symptom was present to indicate its existence. Occasionally, febrile heat, nausea, headache, and thirst were complained of, but not always. Had St. Martin's stomach, and its inflamed patches, not been visible to the eye, he too might have pleaded that his temporary excesses did him no harm; but, when they presented themselves in such legible characters that Dr. Beaumont could not miss seeing them, argument and supposition were at an end, and the broad fact could not be denied."

† Hoppe-Seyler's "Med. Chem. Untersuch.," 1867, p. 257. ‡ Loc. cit.

§ Bernard, "Leçons," 1859, vol. ii. p. 81.

‖ Schiff, Op. cit., Leçon xxxii.

nay be contained in it consequently undergoes only slight and superficial ligestion. If the animal survives the respiratory and circulatory troubles resulting from the operation, a reëstablishment of the digestive power manifests tself after an interval of some days; and the experiments of both Dr. Reid* and Schiff show that when life is sufficiently prolonged, the power of assimiation and absorption is almost completely restored: the evidence of this restoration consisting in the recovery of flesh and blood by the animals, the acidity of the contents of the stomach, and the disappearance of a considerable quantity of alimentary matter from the intestinal canal, with the existence of chyle in the lacteals.† Longet‡ found that milk was coagulated on the second day after the division of the pneumogastrics, and that *small quantities* of meat or other food were digested easily enough, though large masses were only superficially affected. The experiments of Schiff§ seem to prove that the chief *permanent* effect of section of the pneumogastrics is to prevent the stomach from coöperating in the act of vomiting, whilst it does not interfere with the reflex movements of digestion. Both Budge and Schiff maintain that these nerves are the conductors by which *sensory* and *painful impressions* affecting the stomach are conveyed to the mind. The inquiries which have been made in reference to the action of the *Sympathetic* upon the secretion of the gastric juice are, owing to the difficulties which attend experiments upon this point, comparatively few. Budge extirpated the cœliac and meseraic ganglia, and also divided the pneumogastrics, and still found (with one exception) that after the lapse of nine hours the stomach gave an acid reaction; and his results were fully corroborated by Ravitsch,‖ who found that section of the vagi at the œsophageal opening, involving section of the sympathetic, had little or no influence upon either the secretion of the gastric juice or the absorption of the chyme, though the latter was somewhat prolonged: and by Schiff, who divided the splanchnic nerves without effect. Adrian** only obtained negative results as regards the gastric secretion after extirpation of the Cœliac Plexus, which he must have accomplished with great dexterity, as the animals lived for months after the operation.†† The influence exerted by these nerves is probably due to their action on the vessels. Stimulation of the splanchnic nerves induces pallor of the mucous membrane.

119. There can no longer be any doubt that the operation of *Gastric Digestion* is one essentially of *chemical solution;* and that the *vital* attributes of the Stomach are only exercised in the preparation of the solvent, and in the performance of those movements which promote its action on the alimentary matters submitted to it. The first series of facts which clearly demonstrated this position were those that resulted from the very painstaking observations made by Dr. Beaumont in the case of St. Martin already referred-to. By introducing a tube of india-rubber into the empty Stomach, Dr. Beaumont was able to obtain a supply of gastric juice whenever he desired it, the tube serving the purpose of stimulating the follicles to pour forth their secretion, and at the same time conveying it away; and with the fluid thus obtained,

* "Edinb. Med. and Surg. Journ.," April, 1839; and "Physiological, Anatomical, and Pathological Researches," chap. v.—Dr. Reid's results have been confirmed as to this important particular by Hübbenet (Op. cit.) and by Bidder and Schmidt, "Ill. Med. Zeitung," 1852, Heft viii. p. 112.

† For corroborative evidence, see Budge, "Physiologie," 1862, p. 175.

‡ "Physiologie," vol. i. p. 236-7, 1861. § Loc. cit., Leçons xxxi. and xxxii.

‖ "Physiologie," p. 421, 1861; and "Leçons sur la Phys. de la Digestion," 1868, Leçon xxxii. p. 347. ** Eckhard, "Beiträge." Bd. iii. 1862.

†† Bernard, however, states ("Med. Times and Gazette," 1860, vol. ii.) that on galvanizing the sympathetic nerves distributed to the stomach, a sudden arrest of the secretion occurred.

he was able to make various experiments, which showed that the change which it effects upon alimentary matter, when it is kept at a temperature of 98° or 100°, and frequently agitated, is not less complete than that which takes place when the same mattter is submitted to its operation within the stomach, but requires a longer time. This is readily accounted-for when we remember that no ordinary agitation can produce the same effect as the curious movements of the stomach; and that the continual removal, from its cavity, of the matter which has been already dissolved, must aid the operation of the solvent on the remainder. The following is one out of many experiments detailed by Dr. Beaumont:—"At 11½ o'clock A.M., after having the lad fasting for 17 hours, I introduced a gum-elastic tube, and drew off an ounce of pure gastric liquor, unmixed with any other matter, except a small proportion of mucus, into a three-ounce vial. I then took a solid piece of boiled recently-salted beef, weighing three drachms, and put it into the liquor in the vial; corked the vial tight, and placed it in a saucepan filled with water, raised to the temperature of 100°, and kept at that point on a nicely-regulated sand-bath. In *forty* minutes digestion had distinctly commenced over the surface of the meat. In *fifty* minutes, the fluid had become quite opaque and cloudy; the external texture began to separate and become loose. In *sixty* minutes, chyme began to form. At 1 o'clock P.M. (digestion having progressed with the same regularity as in the last half-hour), the cellular texture seemed to be entirely destroyed, leaving the muscular fibres loose and unconnected, floating about in fine small shreds, very tender and soft. At 3 o'clock, the muscular fibres had diminished one-half since the last examination. At 5 o'clock, they were nearly all digested; a few fibres only remaining. At 7 o'clock, the muscular texture was completely broken down, and only a few of the small fibres could be seen floating in the fluid. At 9 o'clock, every part of the meat was completely digested. The gastric juice, when taken from the stomach, was as clear and transparent as water. The mixture in the vial was now about the colour of whey. After standing at rest a few minutes, a fine sediment of the colour of the meat subsided to the bottom of the vial.—A piece of beef, exactly similar to that placed in the vial, was introduced into the stomach, through the aperture, at the same time. At 12 o'clock, it was withdrawn, and found to be as little affected by digestion as that in the vial; there was little or no difference in their appearance. It was returned to the stomach; and, on the string being drawn out at 1 o'clock P.M., the meat was found to be all completely digested and gone. The effect of the gastric juice on the piece of meat suspended in the stomach was exactly similar to that in the vial, only more rapid after the first half-hour, and sooner completed. Digestion commenced on, and was confined to, the surface entirely in both situations. Agitation accelerated the solution in the vial, by removing the coat that was digested on the surface, enveloping the remainder of the meat in the gastric fluid, and giving this fluid access to the undigested portions."* Many variations were made in other experiments; some of which strikingly displayed the effects of thorough mastication, in aiding both natural and artificial digestion.

120. The attempt was made by Dr. Beaumont to determine the relative digestibility of different articles of diet, by observing the length of time requisite for their solution.† But, as he himself points-out, the rapidity of

* Experiments 2 and 3 of First Series.

† It is important to bear in mind that the digestibility of different substances bears no relation to their nutrient value, which is entirely dependent on their chemical composition. Of course, however nutritious a substance may be, it is valueless as an article of diet if it

digestion varies so greatly, according to the quantity eaten, the nature and amount of the previous exercise, the interval since the preceding meal, the state of health, the condition of the mind, and the nature of the weather, that a much more extended inquiry would be necessary to arrive at results to be depended-on. Some important inferences of a general character, however, may be drawn from his researches.—It seems to be a general rule, that the flesh of wild animals is more easy of digestion than that of the domesticated races which approach them most nearly. This may, perhaps, be partly attributed to the small quantity of fatty matter that is mixed-up with the flesh of the former, whilst that of the latter is largely pervaded by it. For it appears from Dr. Beaumont's experiments that the presence in the stomach of any substance which is difficult of digestion interferes with the solution of food that would otherwise be soon reduced. It seems that, on the whole, Beef is more speedily reduced than Mutton, and Mutton sooner than either Veal or Pork. Fowls are far from possessing the digestibility that is ordinarily imputed to them; but Turkey is, of all kinds of flesh except Venison, the most soluble. Perhaps the average period required for the digestion of an ordinary meal, and the complete emptying of the stomach, may be roughly estimated at from 3 to 4½ hours.—Dr. Beaumont's experiments further show that *bulk* is as necessary for healthy digestion, as the presence of the nutrient principle itself. This fact has been long known by experience to uncivilized nations. The Kamschatdales, for example, are in the habit of mixing earth or saw-dust with the train-oil on which alone they are frequently reduced to live. The Veddahs, or wild hunters of Ceylon, on the same principle, mingle the pounded fibres of soft and decayed wood with the honey on which they feed when meat is not to be had; and on one of them being asked the reason of the practice, he replied, "I cannot tell you, but I know that the belly must be filled." It is further shown by Dr. Beaumont that soups and fluid diet are not more readily chymified than solid aliment, and are not alone fit for the support of the system; and this, also, is conformable to the well-known results of experience; for a dyspeptic patient will frequently reject chicken-broth, when he can retain solid food or a richer soup.—Dr. Beaumont also ascertained, that moderate exercise facilitates digestion, though severe and fatiguing exercise retards it. If even moderate exercise be taken *immediately* after a *full* meal, however, it is probably rather injurious than beneficial; but if an hour be permitted to elapse, or if the quantity of food taken have been small, it is of decided benefit. The influence of temperature on the process of solution is remarkably shown in some of Dr. Beaumont's experiments. He found that the gastric juice had scarcely any influence on the food submitted to it, when the bottle was exposed to the cold air, instead of being kept at a temperature of 100°. He observed, on one occasion, that the injection of a single gill of water at 50° into the stomach sufficed to lower its temperature upwards of 30° degrees; and that its natural heat was not restored for more than half an hour. Hence the practice of eating ice after dinner, or even of drinking largely of cold fluids, is very prejudicial to digestion.—Dr. Marcet* suggested, and his suggestion has been adopted with good results, that in cases where the digestive powers are feeble the process of digestion should be carried on to some extent prior to its introduction into the stomach, and for this purpose recommends that to 1 lb. of roast meat finely minced,

cannot be dissolved; but, on the other hand, substances which are very easily digested (such as farinaceous matters) may have a low nutritive value, through containing but a very small proportion of azotized constituents.

* "A New Process for Preparing Meat for Weak Stomachs," 1867.

10 ozs. of a weak solution of hydrochloric acid (containing 232 grains of th pure acid, sp. gr. 1·1496, to one pint of water), 10 ozs. of water and 15 grain of pepsin should be added; the whole being kept for three hours in a ston jar immersed in boiling water. The meat is thus reduced to a pulp, whic will keep for a day or two. When required for use 51 grains of dry Sodiun Carbonate, or 81 grains of crystallized Sodium Bicarbonate must be added It is far from being true, however, that (according to the older view of its power) the Gastric juice is capable of acting upon *all* the nutritive com ponents of the food. The mistake probably arose from the *reduction* to whic these matters are subjected in digestion, the alimentary bolus being completely disintegrated, and its particles saturated with the fluids of the stomach, so tha the whole forms a homogeneous liquid of pultaceous consistence, to whic the name of *chyme* is given. This chyme will, of course, vary greatly in its composition, according to the proportion of the different alimentary substances that have entered into the composition of the food; and its appearance, also, is far from uniform, being sometimes like gruel, but sometimes more creamy, always, however, having a strong acid reaction.

121. Although the *Chyme*, or product of gastric digestion, which escapes through the pyloric orifice into the duodenum, contains much azotized matter in a state of actual *solution*, a considerable proportion of it is still only *reduced* and mechanically *suspended;* and the solution of the latter is continued in the intestinal tube. In the farinaceous part of the food, moreover, no great amount of change has hitherto been effected; and the sugar which has been generated by the agency of the salivary ferment is probably absorbed into the blood-vessels nearly as fast as it is formed. In the condition of the fatty matters no important change is perceptible, except such as results from the solution of the membranes, &c., that enclosed them. Hence we see that the process of Digestion, so far from being completed in the stomach, has only been carried one stage further;* but soon after its entrance into the Duodenum, the chyme is subjected to the actions of the Bile, the Pancreatic fluid, and the Intestinal juice or "Succus entericus" which is secreted by Brunner's glands and the Lieberkühnian follicles. Of these, the *Pancreatic* fluid will be first noticed.

122. In structure the Pancreas closely resembles the Salivary glands (§ 102), though its texture is looser, for it consists of racemose clusters of secreting follicles, so elongated as to be almost tubular, which form the terminations of the ramifying divisions of the duct: each cluster, with its blood-vessels, lymphatics, nerves, and connective tissue, forms a lobule; and the separate lobules are held together by areolar tissue, as well as by the vessels and ducts. The cells lining the acini are arranged in two layers, of which the outer or parietal is composed of slender columnar cells that are transparent, and stain deeply with carmine, whilst the inner or central cells are granular, and stain less deeply. Besides these, fusiform or branched cells are seen here and there in the middle of the acini, which have been named "centro-acinar cells." The processes of these cells penetrate to the wall of the acinus, between the secreting cells, and are believed to act as supporting bodies. Heidenhain† finds that in the fasting condition the granular internal layer of cells occupies the larger, and the homogeneous external layer the smaller part of each acinus. During the first period of digestion, when the liveliest secretion is taking

* During the digestion of vegetable food the Chyme, according to Cl. Bernard (V. Gorup-Besanez, "Phys. Chem.," 1874, p. 305) is alkaline, whilst during the digestion of animal food it is acid.

† Pflüger's "Archiv," Band x. 557.

place, all the cells diminish in size, owing to consumption of the granular internal zone, *with subsequent* increase of the external layer, so that these become enlarged. In the second period of digestion, during which secretion diminishes, and the gland becomes quiescent, new formation of the internal zone takes place at the cost of the homogeneous external zone, which becomes extremely attenuated, and both sets of cells enlarge. In inanition there is gradual increase of the cells to their original size, with slight diminution of the internal zone. Heidenhain thinks that in the living gland-cell in the first instance, not perfect Trypsin, but a mother substance which he terms Zymogen, is prepared, which is soluble in water, and after a time, under the influence of oxygen, sets free Trypsin. Zymogen is probably a combination of Trypsin with an albuminate. During active secretion the amount of Zymogen diminishes, whilst it is stored up again during the period of rest, being most abundant about the fourteenth hour. If the gland be injected from the duct of Wirsung a series of branching tubes is brought into view, which has led various observers* to believe that the secretory cells of the pancreas, like those of the liver, are surrounded by extremely fine ducts, which convey the secretion into the larger excretory passages; others, however, believe that there are no such independent tubes, the appearance being due to the injection forcing its way not only in the axis of the canal, but escaping into the spaces between adjoining cells. Like both the liver and the salivary glands, the *development* of the pancreas commences about the fourth week by the formation of a tubular process of the alimentary canal at a particular spot upon which a mass of cells has previously accumulated. The secretion of this gland resembles saliva in its general appearance, being clear and colourless, of saline taste, free from smell, alkaline in its reaction, owing to the presence of sodium carbonate, and very viscid. Upon the application of heat, or upon the addition of any of the stronger mineral acids, it evolves carbonic acid gas, and coagulates into a solid mass like the white of an egg. This appears to be due to the presence of alkali-albumin and serum-albumin, as well as to a peculiar form of albumin, which is precipitated in a gelatinous condition at a temperature of 32° F. from the concentrated secretion.† The properties of the secretion seem to vary according to the period of digestion at which it is collected, being at first very tenacious, and coagulating completely, and at a later period becoming thinner, more alkaline, and less perfectly coagulable by heat; its solvent powers upon various constituents of food are, at the same time, less strongly marked. Viscid pancreatic juice obtained from the duct contains 90° per cent of water, the remainder consisting of about 9 per cent. of organic substances and about 1 per cent. of ash, seven-tenths of which last is common salt.‡ When the secretion is profuse, the proportion of organic matter diminishes considerably.§ Leucin, Guanin, and Tyrosin, have been stated to be constant constituents of the substance of the gland, and Leucin and Xanthin have occasionally been found in the secretion. Recent experiments, however,‖ render it probable that these substances proceed from the action of the secretion on the albuminous constituents of the blood, or even on the tissue of the gland itself.

* See Langerhans, "Inaug. Dissert.," 1869; "Centralblatt," 1870, p. 261; and Pflüger's "Archiv," Band v. p. 203; Giannuzzi, "Comptes Rendus," t. lxviii. 1869, p. 1280; Saviotti, M. Schultze's "Archiv," Band v. p. 404.

† Wundt. "Physiologie," 1873, p. 217. ‡ For fuller analysis, see Appendix.

§ Weinmann.

‖ Kühne, "Centralblatt f. d. Med. Wiss.," 1867, p. 420; Verhand. Heidelb, "Natur. Hist. Med. Ver.," 1876; and Fudakowski, idem., p. 546.

123. The nature of the organic substance which forms so large a part of the solid residue of the pancreatic juice, and which is so singularly prone to decomposition, has not been accurately determined. Bernard states that it resembles albumen in being precipitated by heat, acids, alcohol, and metallic salts, but differs in being thrown down by sulphate of magnesia, and by the circumstance that, after being precipitated by alcohol, it can be re-dissolved in water. The quantity of the secretion which is poured forth in twenty-four hours has been variously estimated; and perhaps the differences are due, as Bernard has suggested, to the circumstance that when the operation for the formation of a pancreatic fistula has been attended with much violence, when the gland has become inflamed, and the health of the animal has in consequence suffered, the fluid secreted is abnormal, and differs both in quantity and in many of its most essential properties, from the healthy secretion. From these considerations, and from the probably intermittent character of the secretory act, it is manifest that only an approximative estimate of the absolute quantity can be made. Bernard estimates the quantity secreted per hour in the dog, for every 1lb. weight of the animal, at about 15 grains; Schmidt and Kröger at from 20 to 35 grains;* Skrebitzky and Bidder at from 21 to 35 grains. If this last estimate were applied to man, it would give from 12 ozs. to 16 ozs. av. as the total quantity of pancreatic juice secreted per diem, and the pressure under which it is secreted appears to be about 17 mm. of mercury. Bernard describes the gland as pale and flaccid during the period of fasting, and as rosy, but not deep red, some time after food has been taken, when the secretion is rapidly poured forth. The activity of the gland seems to be greatest at the middle or towards the close of gastric digestion,† and at the period, therefore, of the passage of the contents of the stomach into the small intestine. Under the toxic influence of curare, the secretion is greatly augmented. The discharge of pancreatic juice commences as soon as food is introduced into the stomach, and is evidently, therefore, of a reflex nature. The afferent nerve is probably the pneumogastric, and the centre of reflexion is seated in the medulla oblongata, whilst the motor nerves‡ run first in the pneumogastric and splanchnic nerves, and afterwards in the hepatic, splenic, and superior mesenteric plexuses. The secretion may be excited by stimulation of the medulla oblongata, or by direct stimulation of the gland. It may be suppressed by atropin,§ by efforts to vomit, and by stimulation of the proximate stump of the divided pneumogastric, or of the sciatic and other sensory nerves.‖ Section of the nerves accompanying the vessels causes congestion of the gland and a profuse flow of watery secretion (paralytic secretion), which continues even when no food is given to the animal. The nerves terminate, according to Pflüger, in the same way as in the salivary glands, by penetrating the

* See M. Edwards, "Leç. sur. la Physiol.," 1860, p. 522. Colin obtained about 10 ozs. per hour from a cow of medium size and from a horse, but only 3 drachms from a pig.

† Weinmann observed in a dog during the first hour after a full meal 1510 grains secreted whilst after a 45 hours' fast only 7½ grains (Henle and Pfeuffer's "Zeitschrift," N. F. Band iii. p. 247). Kröger obtained 384 grains during the 1st hour, 271 in the 2nd, 225 in the 3rd, 4th, 5th, and 6th, 176 in the 7th, 8th, and 9th, 165 from the 10th to the 14th, and 103 from the 19th to the 24th ("Archiv. Gén. de Méd.," i. 1861, p. 533). Bernstein ("Leipziger Arbeiten," 1870, p. 6) obtained scarcely any from fasting dogs, but remarked a considerable increase (0·6—2·2 cc. in 10 min.) during the 1st hour after feeding, the quantity attaining its maximum at the 2nd or 3rd hour (about 5 cc. in 10 min.), then diminishing to the 5th hour, when a slight increase took place till the 7th hour, after which it gradually fell to zero.

‡ See Afanassiew and Pawlow, Pflüger's "Archiv," Band xvi., 1878, p. 173, and Band xvii. p. 555.

§ Pawlow found this effect in dogs, but not in cats. Ibid., 1878, Band xvii. p. 557.

‖ See Bernstein, Ludwig's "Arbeiten," 1870, p. 1.

secreting cells. It would seem, then, that the gland receives sensory or afferent; motor, secretory, or efferent; and inhibitory nerves; and the general relations of the gland to the nervous system are essentially similar to those of the salivary glands. As the organ is of considerable size, is very constant amongst the Vertebrata, and uniformly discharges its secretion into the duodenum, it is natural to suppose that it must exert an important influence in preparing the food for absorption; and this is fully borne out by our knowledge of the serious interference to the due performance of this function, which results from disease of the pancreas, and of the extreme instability of the organic matter contained in its secretion.

124. It has been already pointed out (p. 69) that three separate hydrolytic ferments are found in the pancreas and the fluid it secretes—*Amylopsin*, which, like diastase, is capable of converting starch into dextrin and a peculiar form of sugar; *Myopsin*, or *Trypsin*, which, like pepsin, can convert the albuminous compounds into peptones; and *Steapsin*, which has the power of breaking up fats, if water be present, into glycerin and the corresponding fatty acids. The amylolytic power* of the pancreatic juice, which resembles, but is much more active than that of saliva, was first observed by Valentin, and may be proved by adding the secretion obtained from a fistulous opening into the duct, or even an infusion of the gland-substance, to either crude or boiled starch; for though the energy of the action is much greater on starch paste, yet even in the case of the raw material, the starch-grains become rapidly altered in form, disintegrated, and dissolved, reducing dextrins, maltose and glucose being successively produced.† The necessity which exists for the conversion of starch into sugar before it can be absorbed renders evident the advantage which attends the presence of a gland possessing a similar transforming power to that of saliva, at some distance from the mouth, where it may act upon crude starch which has been softened, swollen, and otherwise affected by the combined heat and moisture of the stomach. Cane-sugar and Inulin are unaffected by it. Its operation on starch is not interfered with by the presence of the gastric juice, or of the bile. The amylolytic ferment does not appear to be present in the pancreas of the new-born child.‡ Glycogen is acted on much more slowly than starch-paste.

125. The action of the pancreatic juice upon the fats, first demonstrated by Cl. Bernard, is of a double nature. In the first place, it forms with great rapidity, when agitated with them, a remarkably persistent emulsion, and, secondly, it effects their decomposition, providing water be present, into glycerin and the fatty acids. Its action upon Lecithin, a substance that may be regarded as one of the steps in the formation of fats, is the same as on the neutral fats,§ the products being glycerin-phosphoric acid, neurin, and fatty acids. Several hours are required for the process of disintegration, both in the case of fats and of Lecithin, at a temperature of about 100° F.,

* The term "amylolytic," meaning the power of converting starch into sugar, was first employed by M. Foster (Humphry and Turner's "Journal of Anat. and Physiol.," vol. 1866, p. 108). For an attempt to determine the composition of pancreatic ferment, see Liversidge and Clowes, "Journ. of Anat. and Phys.," vol. viii. p. 25.

† In unhealthy conditions of the body it is not unlikely that the same changes may take place in the system as occur when pancreatic juice is allowed to remain long in contact with starch-paste at a moderately high temperature; these changes being accompanied with the evolution of hydrogen, nitrogen, and carbonic acids, indicating the occurrence of the lactic, butyric, or even alcoholic fermentation. See Musculus and de Mering, "Acad. d. Sciences," Jan. 13, 1879.

‡ Korowin, "Centralblatt, f. d. Med. Wiss.," 1873, p. 261.

§ Bokay, "Zeits. f. Phys. Chemie." Band i, 1877, p. 163.

and hence it may to some extent be a putrefactive process.* That this emulsifying action is exerted in the body is shown by the interesting researches of Bernard, who observed that in the Rabbit (in which animal the pancreatic duct discharges itself some inches lower down in the intestine than does the bile duct), when fatty matters have been introduced into the alimentary canal, no considerable change occurs until they have passed the orifice of the pancreatic duct; an oily emulsion being then for the first time apparent, and the opaque whiteness of chyle showing itself in the contents of those absorbents only which originate in the intestinal villi below that orifice. Bernard also pointed out that by putting a ligature round the pancreatic duct, the digestion of oleaginous matter is so completely prevented, that it is found unchanged in the lower part of the intestinal tube, and no opalescent chyle is found in the lacteals. This position is further strengthened by the fact ascertained by clinical observation,† that there is a close relation between disease of the pancreas, and the discharge of fatty matters per anum. Colin‡ (of Alfort), however, made some ingenious experiments, in which he determined the quantity of fat contained in the chyle of cows and other animals, both before and after ligature of the pancreatic duct, and after extirpation of the gland. He was unable to discover any remarkable difference in its composition. Similar experiments were made by Herbst, Schiff, and Donders, from which the conclusion may be fairly drawn, that though the pancreatic juice is of considerable importance in the emulsification of fatty bodies, yet that its action is not indispensably requisite for their absorption; and it is possible, either as Frerichs and Hübbenet state, that the Succus Entericus may possess an emulsifying power of considerable energy, and quite sufficient, in the absence of the pancreatic juice, to prepare a due amount of fat to supply the demands of nutrition; or, as M. Peyrani,§ Voit,‖ and Schiff¶ contend, that the bile is an important agent in the digestion of this class of alimentary substances. In Busch's case, already referred to, the digestive action of the fluid poured forth by the lower part of the Jejunum and Ileum upon fatty bodies introduced into them through the fistulous orifice, was exceedingly imperfect. Steapsin or the fat decomposing ferment exists in the pancreas of the new-born child. It is not soluble

* Brücke ("Wiener Sitzungsber." Band lxi. 1870, Abtheil. ii. p. 362) has shown that oil mingled with dilute albumen, with fresh ox-gall still containing mucus, or with a dilute solution of borax, or sodium-carbonate, is much more easily and completely emulsified if, instead of being perfectly pure, it is somewhat rancid—that is to say, has been partly converted into, or contaminated with, the fatty acids. Pure and neutral oil, shaken up with either of these fluids, forms relatively large drops which rapidly reunite, but if mingled with fatty acids it forms after the first agitation a white milk. It would appear that whilst sodium-carbonate has little action in emulsifying fat, yet if free acids be present, these combine with a part of the soda to form a soap, which effects the emulsification of the oil. The same fact can be shown in another way by adding a small quantity of a solution of soap to pure oil, when an emulsion can be quickly made; and J. Gad ("Archiv f. Anatomie u. Physiologie, His. and Braune," 1878, p. 183) has pointed out that the mere contact of rancid oil with an alkaline solution causes an emulsion to be gradually formed, the particles near the line of contact of the two fluids being thrown into violent rotatory movements, and the emulsion being of the finest possible character. The drops soon begin to exhibit peculiar movements, sending out processes which after giving off a white milk are again drawn in, some small droplets separating, and the original drop assuming again a round form. If these separated particles be collected and immersed in another fresh portion of soapy fluid no new movements are observed.

† See Dr. Bright's researches on this point, in "Med.-Chir. Trans.," vol. xviii.; also an Article on Pancreatic Disease and Fatty Discharges, in "Brit. and For. Med.-Chir. Rev.," vol. xii. p. 154. ‡ "Comptes Rendus," 1856. § "Comptes Rendus," 1867, p. 197.

‖ See Brücke, "Vorlesungen," 1874, p. 329.

¶ "Centralblatt," 1872, p. 790, Schiff occludes the duct of Wirsung with paraffin, and finds the digestion of fats in no way interfered with.

glycerin, but is precipitated when burnt magnesia is added to the pancreatic juice.

126. Lastly, as originally stated by Corvisart,* healthy pancreatic juice, or the infusion of a healthy pancreas, or even a solution of precipitated pancreatin in distilled water, possesses a distinctly solvent action on albuminous compounds, converting them into peptones without the supervention of any signs of putrefaction. This action so far differs from peptic digestion that whilst pepsin converts albuminous compounds at once into acid-albumin, myopsin converts them without any previous process of swelling up into globulin, and then into true peptones which appear to be identical with the peptones found in gastric digestion.† The previous action of hydrochloric acid does not facilitate, but, on the contrary, rather impedes the action of myopsin or trypsin. The presence of oxygen gas is not required for the formation of the globulin substance.‡ The action seems to be one of a corrosive nature, the albumin breaking up into flocculi, which gradually dissolve till the fluid only presents a slight degree of turbidity. Various agents that are fatal to the lower forms of organic life have little influence on the disintegrating process exerted upon albuminous compounds by myopsin, or perhaps only somewhat retard this action. Thus arsenious acid and its salts,§ ether, and salicylic acid, unless very concentrated,‖ interfere but little with it. Antipepton, Tyrosin, and Leucin are largely formed during the action of pancreatic juice on proteids, the two latter substances more rapidly than in peptic digestion, but Indol is a product of their putrefaction.¶ Asparaginic acid is one of the products of the digestion of fibrin and glutin,** and may be an intermediate stage between albumin and urea. Gelatin is rendered fluid and soluble and dissolved, but nuclein and hæmoglobin resist solution. It is noticeable that the substances just mentioned as resulting from the action of myopsin on albuminous compounds contain progressively smaller quantities of nitrogen; albumin containing 15·17 per cent. of its weight of nitrogen; leucin, 10·7; asparaginic acid, 10·5; and tyrosin, 7·74. The following experiment performed by Meissner demonstrates the action of the pancreatic juice in the living body:— The duodenum in a dog was thoroughly washed out with a stream of warm water, and surrounded by a ligature above and below the point of entrance of the large duct of the pancreas. By this proceeding the entrance of the secretion of the superior duct, and of the bile through the ductus communis choledochus, was excluded. And now, the animal having previously been kept fasting for fifteen hours, 34 grammes of hard-boiled white of egg were introduced into the loop of intestine confined between the ligatures, whilst 20 grammes were at the same time introduced into the stomach, to supply the ferment with which he believed it to be requisite that the pancreas should be charged. After the lapse of fifteen hours the duodenum was examined, when 150 grammes of neutral fluid were found quite free from any odour of putrefaction, with 4 grammes of undissolved albumen; 30 grammes of this substance had consequently been dissolved. All observers are agreed that the most active pancreatic juice is

* "Sur une Fonction peu connue du Pancreas," Paris, 1857-58.

† See Hoppe-Seyler, "Physiolog. Chemie.," 1878, p. 264. Kistiakowski, however, believes that they contain more carbon and oxygen, and obtained on analysis the following per-centage result:—C 42·7, H 7·13, N 15·92, O 33·2, S 1·03.

‡ Hüfner, "Journ. f. prakt. Chemie," N.F. Band x. p. 1. Schäfer and Böhm, "Wurzburg Yerhand.," 1872, Band iii. p. 238.

§ Hoppe-Seyler, "Phys. Chemie," 1878, p. 264. ‖ Kühne, Op. cit.

¶ Kühne "Ber. d. Deutsch. Chem. Gesells.." 1875, Band viii. p. 208. Nencki, "Ueber die Zersetz. der Gelatin.," &c., Bern, 1876, p. 31.

** Knieriem, "Zeits. f. Biologie," Band xi. p. 198. Weiske, idem, Band xv.; 1879, p. 260.

obtained from an animal in full digestion, as it is only at that time that the gland is thoroughly charged with the pancreatic ferment that is capable of digesting albuminous compounds. In new-born animals, and in conditions of gastric disease in which the normal acid secretion in the stomach is interrupted, pancreatic digestion may take place in the stomach,* giving rise, as has been frequently observed, to fatty infiltration of the epithelial cells lining the stomach, and repletion of the gastric lymphatics with chyle. Hoppe-Seyler states that he has observed pancreatic digestion in the matters vomited by a patient with gastric disease, strong peptic digestion occurring as soon as they were acidified with hydrochloric acid. In the later stages of pancreatic digestion sugar disappears, and it is probable that bacteria are normally produced. In a remarkable and well-observed case of atrophy of the liver and pancreas described by Dr. J. A. Flés, a considerable quantity of fat and undigested muscular fibre was found to pass away in the fæces, but after the daily administration of a calf's pancreas nearly all the *fat* and a great proportion of the *muscular tissue* disappeared.†

127. The Duodenum receives not only the Pancreatic, but also the *Biliary* secretion; and from the constancy with which this fluid is poured into the upper part of the intestinal tube, or even into the stomach itself, in all animals which have any kind of hepatic apparatus, it seems a legitimate inference that this secretion is not purely excrementitious, but serves some important purpose in the digestive process. It is not easy, however, to state with precision what this purpose is. The results of many of the experiments which have been made to determine it are vitiated by the fact, that the pancreatic duct in most cases discharges itself into the intestinal tube at the same point with the hepatic, and has thus been frequently involved in operations performed upon it.—As the most important constituents of Bile, and the agency of the Liver as an assimilating and depurating organ, will be more appropriately considered elsewhere (CHAPS. VI. and XI.), we shall here limit ourselves to the consideration of what may be regarded as the best-established facts in regard to the uses of the biliary secretion in the digestive process.

128. When Bile is mingled with fresh or artificial gastric juice, a precipitate falls which partly consists of glycocholic acid,‡ partly of albumin rendered insoluble by the taurocholic acid, of mucin and the colouring matter of the Bile, and partly of pepsin, which attaches itself to the precipitate.§ Dr. Dalton,‖ however, states that Bile does not form a precipitate with gastric juice holding albuminose (peptones) in solution. These fluids are therefore not finally antagonistic to each other in the digestive process, though at first they produce a precipitate on admixture.¶ When its action is tested out of the body, by mingling it with the different constituents of food, it is found to exert a slight but distinct action in converting starch into sugar.** It therefore

* Hoppe-Seyler's "Physiologische Chemie," 1878, p. 328.

† Donders' "Archiv," 1862, Band iii. pt. ii. p. 187. A practical application of the digestive powers of the pancreatic secretion has been made by Dr. Dobell, who uses an emulsion of the fresh gland in certain forms of indigestion. A combined solution of pepsin and pancreatin has also been used with good effect by Mr. Kinkead. See "Lancet," 1870, ii. p. 667.

‡ See Burkhart, in Pflüger's "Archiv," 1868.

§ Hammarsten, Pflüger's "Archiv," 1870, p. 53.

‖ "Human Physiology," 5th edit. 1871, p. 181.

¶ See also Schiff, Pflüger's "Archiv," 1870, p. 620.

** v. Gorup-Besanez, 1862, p. 467. See v. Wittich, Pflüger's "Archiv," 1872, Band vi. p. 184.

contains a diastatic ferment. It has no action upon cane-sugar, until it has stood a considerable length of time; but then it converts it into lactic acid. This change it speedily exerts, as do many other animal substances, upon grape-sugar. It has no action on albuminous substances, even when acidulated. When mingled with neutral oils or fats it forms with them a finely granular emulsion, well adapted to penetrate into the interior of the body, through the channels that will be hereafter described in the walls of the intestine; but if added to the fatty acids the biliary salts are decomposed, the glycocholic and taurocholic acids are set free and the soda uniting with the fatty acids, forms easily soluble soaps, which last may again augment the emulsifying power of the undecomposed bile. Wistinghausen* and Hoffmann† have shown that the force requisite to effect the filtration of an oily substance through an animal membrane is much less when the membrane is moistened with an alkaline fluid, or with bile, than when it is moistened with pure water. Bile certainly possesses an *antiseptic* power, for M. Bernard found that when two similar pieces of meat had been immersed for three months, one in a bottle of gastric juice alone, and the other in a mixture of gastric juice and bile, a strong ammoniacal odour resulting from decomposition was emitted from the former, whilst the latter was pure and free from any smell whatever. The difference is even more marked if an infusion of pancreas be used instead of the gastric juice. And it was remarked by MM. Tiedemann and Gmelin (and also recently by Hoffmann), that when the bile was prevented from passing into the alimentary canal, the contents of the latter were more fœtid than usual. Moreover, it is found that the admixture of bile with fermenting substances checks the process of fermentation; and M. Bernard‡ has shown by ingeniously-contrived experiments, that this power is exerted also to some extent in the living body. Hence we can understand how the reflux of bile into the stomach should seriously interfere with the process of gastric digestion;§ and how, when there is a deficient secretion of bile or more food is swallowed than the bile provided for it can act upon, or the character of the biliary secretion itself has undergone any serious pervertion, there should be much more than the normal amount of putrefactive fermentation, as is indicated by an evolution of flatus, and very frequently by diarrhœa. Schiff‖ and Budge¶ have shown that the bile produces energetic, and indeed almost tetanic spasms of the muscles, both voluntary and involuntary, when applied either to the tissue itself or to the nerves supplying it. Its importance, therefore, in maintaining the *peristaltic action of the intestine* is probably considerable, whilst by exciting the involuntary muscular fibre-cells of the villi it very probably materially aids the movement of the chyle in the lacteals. Moreover, the presence of a proper quantity of bile in the intestine seems to promote the secreting action of the intestinal glandulæ: this appears from the tendency to constipation which is usually consequent upon deficiency of the secretion, and from the diarrhœa which proceeds from its excess; and is confirmed by the purgative properties which inspissated

* "Endosmotische Versuche," Dissert. inaug., Dorpat, 1751. See also Dr. Charles Williams, in Prize Essay of the Boylston Med. Soc. 1874. Supplement to "Boston Med. Surg. Rep.," 1874. For some strictures on Wistinghausen's experiments see Quincke, Pflüger's "Archiv," Band xix. 1879, p. 139.

† "Ueber die Aufnahme von Quecksilber," 1854, Wurzburg.

‡ "Amer. Journ. of Med. Sci.," Oct. 1851, p. 351.

§ The reflux of bile into the stomach, however, appears to be normal in Birds. Hoppe-Seyler, "Phys. Chem.," 1878, p. 328.

‖ "Archiv für Phys. Heilk.," Band ix. p. 60.

¶ "Physiologie," 1861, p. 195.

ox-gall has been found to possess. The value of the bile in the preparation and absorption of fats in digestion is shown by the fact that animals in which a biliary fistula has been established so that the bile escapes without entering the alimentary canal become thin, fail to take up more than one-fifth or one-seventh of the usual amount of fat, have transparent chyle, and discharge fat with the fæces. They may, however, live for months or even years* if supplied with a sufficient amount of food, for the appetite is greatly increased.

129. The best evidence that has hitherto been obtained of the quantity of Bile daily poured into the alimentary canal of man has been afforded by patients suffering from fistula of the cystic, or of the common bile duct. In one of these cases which was under the observation of v. Wittich† the quantity discharged amounted to 22·2 c.c. per hour, or 532·8 cub. cent., which are equivalent to one pint, in 24 hours. In another case observed by Westphalen‡ a man weighing about 140 lbs. discharged almost exactly the same quantity (7703 grains = 1 lb. 703 gr. av., or about one pint) with but small variation daily for 10 days. Nasse and Plattner§ obtained from a dog 105 grains, and Stackmann 108 grains per diem, for every 1 lb. of body weight. Bidder and Schmidt, from experiments on a dog, estimated the quantity in man at $3\frac{1}{2}$ lbs. daily, but such experiments have been shown by the Edinburgh Committee of the British Medical Association to afford no reliable data for comparative estimates, since the size and weight of the animals have no relation to the amount of bile secreted. In one instance a large dog weighing 42 lbs. secreted on an average only 1036 grains daily, while a dog weighing 11 lbs. secreted 1857 grains daily.‖ Schiff¶ has shown that a much larger quantity of bile is discharged into the duodenum under normal conditions than can be collected from a biliary fistula, the reason being that the bile is reabsorbed with great rapidity and is again excreted, together with fresh bile, by the liver. This observation has been confirmed by Laffter,** under Heidenhain's direction, the evidence relied on being the injection of bile into the duodenum, when its quantity was observed to be increased, and the injection of coloured bile or rhubarb into the intestine, which reappeared in the course of a minute in that flowing from the canula. Wolf†† found that the amount of secretion in dogs was proportional to the size of the liver; that it was more active in small and young animals; that it was most abundant on mixed diet (rising with the quantity of meat); less on a diet of bread or rice, and least on a diet of fat; and that it was greater by day than by night. It is augmented after ingestion of water though it is then of poorer quality, and also after vegetable diet. The quantity secreted by Herbivora is much greater than by Carnivora.

* At the meeting of the French Academy, June 23, 1851, M. Blondlot gave the history, and an account of the post-mortem examination of a dog that had lived five years without the passage of any bile into the intestinal tube. For the effects of Ligature of the Bile Ducts see Legg, "St. Barth. Hosp. Rep.," vol ix. 1873, p. 161.

† Pflüger's "Archiv," Band vi. 1872, p. 181.

‡ "Deuts. Archiv f. klin. Med.," 1873, Band xi. p. 588.

§ Béclard's "Physiologie," 1862, p. 501.

‖ See report by Drs. Bennett, Rutherford, and Gamgee, in "Trans. of British Assoc. for the Advancement of Science," 1868. The experiments of this Committee, which was appointed for the purpose of determining the action of Mercury, &c., on the Liver, showed conclusively that in dogs with biliary fistulæ the administration of mercury does not cause any increase in the amount of bile secreted or discharged, while if it cause purgation or impairment of health, the quantity is diminished. Taraxacum did not cause augmentation of the secretion. See also Brunton "on Purgation," in "Practitioner," 1874.

¶ Pflüger's "Archiv,' 1870, p. 568. ** See Laffter, "Inaug. Dissert.," Breslau, 1873.

†† "Centralblatt," 1869, p. 86.

Prof. Rutherford has found, in an extensive series of experiments, that the secretion of bile is increased in dogs by the administration of podophyllin, rhubarb, aloes, colchicum, enonymin, sanguinarin, iridin, ipecacuan, colocynth, jalap, sodium sulphate, potassium sulphate, sodium phosphate, Rochelle salt, nitro-hydrochloric acid, and corrosive sublimate. It is not increased to any material extent by croton oil, magnesium sulphate, sodium chloride, potassium bicarbonate, ammonium chloride or calomel, and as a rule severe purgation diminishes the flow of bile.* Wolf in Man and Arnold† in Dogs found that the activity of the liver attained its maximum an hour or two after food, Voit‡ two hours after, Kölliker and Müller between the 6th and 8th hours, Bidder and Schmidt§ about 10 or 12 hours after a full meal, and Dr. Austin Flint‖ from the 2nd to the 8th hour.—As Dr. Dalton has remarked, a distinction should be drawn between the time at which the largest quantity of bile is discharged into the intestine, and that at which the secretory activity of the liver is at its height. In his own experiments on a dog, which appear to have been conducted with much care, a considerable quantity of bile was discharged into the intestine soon after feeding, as is shown in the following Table:—¶

Time after feeding.	Quantity of fluid in 15 minutes.	Dry residue of the same.	Quantity of biliary matter.	Proportion of biliary matter to dry residue.
Immediately	640 grains.	33 grains.	10 grains.	·30
1 hour	1990 „	105 „	4 „	·03
3, 6, 9 hours	780, 750, 860 „	60, 73, 78 „	4, 3½, 4½ „	·07, ·05, ·06
12, 15 „	325, 347 „	23, 18 „	3¾, 4 „	·16, ·22
21, 24, 25 „	384, 163, 151 „	11, 9½, 5 „	1, 3¼, 3 „	·09, ·34, ·60

The secretion diminishes considerably when food is withheld for some time; the quantity poured-out after ten days' starvation being only about one-eighth of what it is when at its maximum. Still it is obvious, that although its rate is thus greatly influenced by the stage of the digestive process (which is the less to be wondered-at, when it is remembered that the secretion is formed from blood that is charged with newly-absorbed and imperfectly-assimilated matters), the excrementitious character of the secretion requires that its elimination shall be constantly going-on to a certain degree; but a receptacle is provided in Man, as in most others among the higher animals whose digestion is performed at intervals, for the storing-up of the fluid until it can be usefully employed in that process. The intestinal orifice of the ductus choledochus is closed by a sort of sphincter; and the fluid secreted during the intervals of digestion, not being propelled with a force sufficient to dilate this, flows back into the gall-bladder, which dilates to receive it. According to Friedländer and Barisch** the pressure under which bile is secreted is very low, not much exceeding the blood pressure, or about 200 mm. of water, or 16 mm. of mercury. The presence of food, and especially of the acid products of gastric digestion, in the duodenum seems to excite the walls of the gall-

* Rutherford and Vignal, Humphry's "Journ. of Anatomy," vol. x. 1876, p. 253; and vol. xi. 1877, pp. 61 and 625; and "Brit. Med. Journ.," 1878.

† "Zur. Phys. der Galle," Mannheim, 1854.

‡ "Phys. Chem. Untersuchungen," Augsburg, 1857, p. 41.

§ "Verdauungssäfte und Stoffwechsel," §§ 114-209.

‖ "Physiology of Man," 1867, part ii. p. 375.

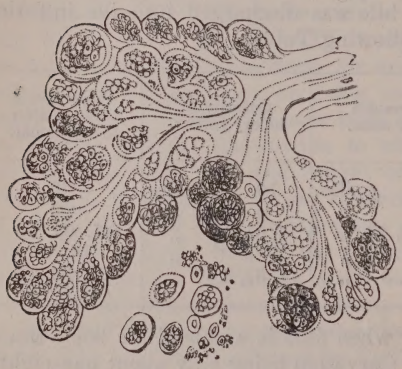
¶ Dalton, "Phys.," 1871, p. 178.—The dog in these experiments weighed 36½ lbs.

** Dubois Reymond's "Archiv," 1860, p. 646.

bladder and of the biliary ducts* (which contain a large quantity of non-striated muscular fibre), to a contraction sufficiently powerful to propel their contents into the intestine, in spite of the opposition of the sphincter; but whether this takes place through a reflex action of the nervous system, or through the direct stimulation of the muscular coat of the duct by the passage of alimentary matters over its orifice, we have at present no means of satisfactorily determining. It will be recollected that the gall-bladder is usually found distended with bile, in cases of death from starvation (§ 79), notwithstanding the diminution in the amount actually secreted. Of the bile which is poured into the intestinal tube, by far the greater proportion seems to be re-absorbed (§ 134), or at least to be so altered that the presence of the biliary acids can no longer be recognised.

130. Besides the biliary and pancreatic secretions, there is poured into the Intestinal canal a fluid secreted in its own walls, which has received the designation of *Succus Entericus*. The secretion of this fluid is partly the function of the Glands of Brünner, which are small, elongated racemose, or tubular glands† (Fig. 75), imbedded in the walls of the duodenum, and extending to the commencement of the jejunum, but chiefly of the follicles of Lieberkühn, with which the intestinal canal is furnished throughout its entire length. The cells lining Brünner's glands‡ are columnar in form, but destitute of a membrane, and have a lateral process at their attached extremity, near which the nucleus is situated. The nucleus is not apparent in fresh preparations. The cell-contents consist of proteids, mucin, a substance which is soluble in a 10 per-cent. solution of sodium chloride and is precipitable by alcohol, fat drops, and granules. The cells are small and cloudy in fasting, but large and bright during digestion. The secretion of the glands cannot be obtained separately during life, but when dissected out it is found that their watery extract converts starch into dextrin and sugar,§ dissolves fibrin, but not albumin at 35° C. (95° F.), and has no action on fats. Grützner‖ was unable to obtain any diastatic action with the extract, but found that it resembled pepsin in dissolving the proteids. The glands of Lieberkühn are

Fig. 75.



Portions of one of *Brünner's Glands*, from the Human Duodenum.

* Bernard and Küthe (Canstatt's "Jahresbericht," 1861, p. 131) found that touching the point of entrance of the biliary duct into the intestine with an alkaline fluid had little or no effect, whilst brushing it lightly over with an acid solution immediately caused a discharge of bile to take place.

† Puky Akos and Schlemmer ("Wien Akad. Sitzungsber.," 1869, Band lx. p. 31, and p. 169), and Renaut, "Soc. de Biol." Mars 8, 1879, regard these glands as belonging rather to the tubular than to the racemose type, whilst Schwalbe considers them to be intermediate to both. See Max Schultze's "Archiv," Band viii. p. 92. Toldt ("Mittheil. der ärtz. Vereins in Wien," Band i. p. 33) holds them to be racemose glands.

‡ According to Schwalbe, "Archiv f. Mic. Anat.," Band viii. p. 92, 1871.

§ Krolow, "Berl. Klin. Wochens.," 1870, No. 1

‖ Pflüger's "Archiv," Band xii. p. 228.

straight narrow cæca, standing side by side, with a little intervening adenoid substance (except where the Peyerian bodies lie amongst them), and corresponding in length with the thickness of the mucous membrane. They are lined by columnar epithelium. Their orifices are seen in the interspaces between the villi, where they are so closely set-together as to seem like the apertures of a sieve; and they are arranged in rings around the Peyerian glandulæ. Brünner's glands resemble the pancreas in structure. The cells become large and transparent during digestion. It has been found* that a glycerin extract of the glands when dissected out possesses both a peptic and a diastatic action, dissolving albumins and converting starch into sugar, but it had no action on fat. Costa found that glycerin extract of Brünner's glands, and of the Lieberkühnian follicles of the Horse possesses a diastatic action, but has no action on albumin or fat.

The *Intestinal juice*† appears to be a colourless viscid liquid, invariably alkaline in its reaction, and containing from 3 to $3\frac{1}{2}$ per cent. of solid matter. Its sp. gr. is about 1011. The total amount daily secreted in Man has been estimated at about 7 ozs.; the rate of its secretion seems to be most rapid five or six hours after a meal; and its quantity decreases during sleep. The most satisfactory observations that have been made in regard to the properties of the succus entericus or secretion of the mucous membrane of the small intestine are those of Busch‡ upon a patient with an intestinal fistula. In Busch's case, in which the contents of the stomach and duodenum were completely prevented by a fistulous opening from entering the small intestine, it was clearly determined by analysis of the fæces, as well as indicated by the great improvement in the health which resulted from introducing food into the lower part of the intestine, that the fluids secreted by the jejunum, ileum, and large intestine were capable of dissolving albumen (though with the evolution of a putrefactive odour, probably due to the absence of the bile) and of converting starch into sugar. There seemed, however, to be little or no emulsifying power exerted on the fats, which were also but very slightly absorbed, the greater part reappearing in the fæces. In this case the woman lived for six weeks, previous to her coming under the care of M. Busch, upon the absorption which had taken place in the stomach and duodenum. A great portion of the products of digestion, which presented a variable reaction to test-paper, flowed off by the fistulous orifice, and she had become much emaciated. The treatment adopted was the re-introduction of this discharged fluid into the lower orifice of the fistulous opening, when she rapidly regained her health and strength. In M. Demant's case, in which a segment of the intestinal canal was isolated, the succus entericus contained no peptic or albumin-digesting ferment, as it was without action on any of the proteids; but it contained a diastatic ferment, since it converted starch into grape-sugar. It converted cane-sugar into grape-sugar, but did not act on Inulin. Fats containing free acids were emulsified, but neutral fats were unacted on. Many experiments have been made upon animals. Thiry§ isolated a loop of the small intestine in a dog preserving the vascular supply intact, and established a fistulous opening between it and the surface. The quantity of fluid obtained in this way from the loop, if calculated for the whole length of

* Krolow, "Berlin, Klin. Wochenschrift," 1870; Costa, "Centralblatt," 1870, p. 561.

† Bidder and Schmidt, §§ 260–282; and Lehmann's "Physiologischen Chemie," 2nd edit., Band ii. pp. 95–99.

‡ Virchow's "Archiv," Band xiv. p. 140, and Bernhard Demant, "Centralblatt. Med. Wiss.," Feb. 15, 1879.

§ "Sitz. d. k. Akad. zu Wien," Band i.

the intestine, amounted to about 1 lb. in five hours, and was of a clear straw-yellow colour, alkaline reaction, and exceedingly constant specific gravity (1·0115). It contained about 2·5 per cent. of solids, less than one-half of the amount obtained by M. Busch from his patient, of which about 1·5 consisted of albumin and other organic matters, the remainder being salts. In experimenting on the physiological effects of this fluid upon the different constituents of food, little more than negative results were obtained, no action being apparently exerted either on starch, fat, or albumin, and only a feeble power (when alkaline) of dissolving fibrin. Paschutin,* operating in a similar manner, obtained a fluid which had little or no action on any of the fats nor on the various albuminous compounds. The *infusion* of the small intestine converted starch and cane-sugar into a form of grape-sugar.† Dobroslawin‡ pursuing Thiry's method in Dogs found that the fluid secreted possessed a diastatic action on starch, requiring, however, about two hours to operate, and had a slow and feeble action on raw fibrin, which at a temperature of 100° F. was converted into peptone in the course of from 20 to 48 hours without the occurrence of any putrefactive odour. It had no action on oleaginous compounds. Schiff§ also operating after Thiry's method upon Dogs found that small portions of albumen, casein and fibrin, generally underwent conversion into peptones, and that starch was rapidly converted into sugar. Occasionally, however, perhaps owing to peculiar states of the animal's health, or to the immediate effects of the operation, these actions failed to take place.‖

131. Under normal conditions the fluid contents of the small intestines is a mixture of the salivary, gastric, biliary and pancreatic secretions with the secretion of the intestinal glandulæ, and there can be little doubt that in this part of the alimentary canal all the principal constituents of the food are reduced to a soluble condition. Here the conversion of starchy into saccharine matter is completed, the oleaginous compounds are emulsified and in part saponified, and a solvent agency is exerted even upon albuminous substances which have not been submitted to the previous agency of the gastric fluid (as has been shown by experimentally introducing pieces of meat, through a fistulous orifice, directly into the duodenum).¶ The contents of the intestines, which are highly acid in the first part of the duodenum, become gradually neutralised and then alkaline by admixture with the secretions of the liver and pancreas, but towards the lower part of the ileum it has been found that owing to lactic and butyric acid fermentations, the chyme becomes acid though the mucous membrane is alkaline to test-paper.** In a case recorded by Lossnitzer an opening existed twelve inches above the ilio-cæcal valve. After a meal of milk, bread, and a little meat, the chyme was turbid, flocculent, bright yellow, rather strongly acid, foaming, smelt of volatile fatty acids, and on standing

* "Centralblatt," 1870, p. 561.

† The infusion of the small intestine of the sheep and calf is incapable of converting cane-sugar into grape-sugar.

‡ "Untersuch. aus d. Instit. für Physiologie in Graz," 1870. Dobroslawin obtained in one case 34 grains of fluid per hour from a loop of intestine about 13 inches in length; and in another case 28 grains of fluid from a loop about 19 inches in length. The rapidity of secretion was augmented by the passage of a current of electricity. See also Eichhorst.

§ Abstract in Henle and Meissner's "Bericht," 1868, p. 168.

‖ Quincke also frequently observed the solvent action of the succus entericus upon fibrin to fail.

¶ See the account of M. Cl. Bernard's researches in the "Amer. Journ. of Med. Sci.," Oct. 1851, p. 356; Zander, "De Succo Enterico," Inaug. diss., Dorpat, 1850; and Frerichs, art. *Verdauung*, in Wagner's "Handwörterbuch," Band iii.

** Braune, "Archiv Gén. de Médecine," 1861, p. 610, and Lossnitzer, "Henle's Bericht," 1864, p. 250.

uickly developed gas bubbles. The fluid contained biliary acids and peptones, ut neither parapeptone nor sugar.

132. The action of the Pancreatic secretion on albuminous compounds, s already stated, terminates with the production of Leucin, Tyrosin, and sparaginic acid in the small intestines. The further changes taking place in the ower part of the ileum and in the large intestine which result in the formation f the ill-smelling compounds Indol, Skatol, and Phenol, are essentially the result f putrefactive fermentation accompanied or induced by the presence of bacteria nd other low organisms, which have been probably for the most part introuced from without. Various acids, as lactic, acetic, butyric, and baldrinic, together with glycin and certain gases, as CO_2, H_2S, H and CH_4, also make heir appearance. It is to the above acids that the acidity of the contents of he cæcum, so strongly marked in Herbivora, is usually due. In Carnivora, ccording to Bernard,* they have an alkaline reaction. That digesion of albuminous compounds will still take place, though imperfectly, n the large intestine, is shown by the observations of Steinhauser† upon a woman who had an artificial anus communicating with the large intestine. When food was introduced into the lower part of the bowel, it was for the most part discharged unaltered; but albumin was to some extent dissolved. Czerny and Latschenberger‡ have more recently had a similar opportunity in a patient who after Hernia had a fistulous orifice in the sigmoid flexure. Their experiments led them to the conclusion that although the lower part of the sigmoid flexure and the rectum in Man have no digestive power on albumin or fibrin, and no power of emulsifying fats, yet that soluble albumin and fat in the state of emulsion may there undergo *absorption* in an unaltered condition. Starch-paste was also absorbed, but they were unable to satisfy themselves whether it was first converted into sugar. The addition of common salt or of magnesium sulphate checked or altogether prevented absorption. Markwald§ experimented on a case of fistula (following hernia, patient being forty-nine years of age) of the cæcum, and had thus the whole tract of the large intestine at his disposal. The temperature of the large intestine, which was thoroughly healthy, was 37·6° C., the peristaltic movements were active. When sponges were introduced and left for two hours, a somewhat tenacious slightly-cloudy fluid of strong alkaline reaction was obtained, containing a trace of albumin which was without the slightest diastatic action on starch. Starch-paste introduced in gauze bags exhibited no conversion into sugar, even after four to six hours. When fibrin and coagulated white of egg were introduced they underwent considerable diminution (84 per cent. in twenty-six hours in the case of fibrin); putrefactive decomposition or fermentation then set in, with the production of Peptone, Tyrosin, and Indol. Absorption of peptones, as indicated by an increase of the urea, occurred late and only to a slight extent, and even water was but slowly absorbed. That the large intestine is not essential to life and health is shown by this case, in which the patient was in fairly good health after two and a-half years. Leube‖ found in a patient with Cancer of the Intestine, that whilst albumin underwent no digestive action, when introduced *per se* into the bowel, raw starch, a mixture of finely-minced meat and pancreas acquired the smell, consistence, and appearance of ordinary fæces after it had been retained in the bowel for about

* Bernard, "Liquides de l'Organisme," 1859, p. 39; see also Blondlot, "Traité de la Digestion," p. 103.

† See Milne Edwards, vol. vii. p. 136, 1862.

‡ Virchow's "Archiv," Band lix. 1874, p. 162.

§ Virchow's "Archiv," Band lxiv. p. 505.

‖ "Sitzungsbericht d. Phys.-Med. Soc. zu Erlangen," 5th Dec. 1871.

twenty-four hours, and in a later communication* he recommends the employment of such a mixture with the glycerin extract of the pancreas as a means of supporting life, especially during the summer months, when the fresh gland and its juice soon lose their digestive properties by putrefaction.

133. The undigested residue of the food, mingled with the products of secretion that have been poured into the alimentary canal, gradually acquires, in the large intestine, the ordinary consistency of Fæces, through the continuance of the absorbent process, whereby the superfluous fluid is removed. The condition of this residue has been particularly studied by Dr. Rawitz and Dr. Marcet.† By the former observer, muscular fibres are stated to be almost entirely dissolved, especially in the case of fish and the hare, though less rapidly in that of poultry and other animals, only a few fragments remaining. Dr. Marcet, however, found muscular fibres, exhibiting clearly their well-marked structure, almost constantly present and in considerable quantities; and he is inclined to believe that when meat is daily taken, only the juices are extracted, the fibres themselves undergoing but little digestive action. The cells of cartilage and fibro-cartilage, the fibres of elastic tissue,‡ mucin, nuclein, and fatty matter if taken in excess, are frequently found unchanged in the fæces; and crystals of cholesterin may usually be obtained, especially after the use of pork fat.—"As regards *vegetable* substances, Dr. Rawitz states that he frequently found large quantities of cell-membranes unchanged in the fæces; also starch-cells (which were rarely seen by Dr. Marcet), deprived of only part of their contents. The green colouring principle, chlorophyll, was usually unchanged. The walls of the sap-vessels and spiral vessels were quite unaltered by the digestive fluid, and were usually found in large quantities in the fæces; their contents, probably, were removed."§—Besides the undigested residue of the food, the microscope enables us to recognise the brown colouring-matter of the bile, epithelium-cells and mucus-corpuscles, and various saline particles, especially those of the ammonio-magnesium phosphate,‖ whose crystals are well-defined; most of which are derived from the secretions.—The quantity of fæcal discharge which is daily passed by an adult seems to vary from 2 to 10 ozs. Dr. Edward Smith found the average weight in prisoners at the Coldbath Fields Prison to be 8·55 oz.¶ These men were fed upon a full dietary with brown bread, and the proportion of the fæces to the solid food was 1 : 4·5. Severe labour on the treadmill was found to diminish the quantity of fæces, whilst the rest of Sunday occasioned a considerable increase. The proportion of water was very uniform—viz., 73·5 per cent.; and an average of 41·8 grains of nitrogen

* "Centralblatt," 1872, p. 465. † "Med. Times and Gaz.," July 31, 1858.

‡ It has been pointed out to the Author by his friend Mr. Quekett, that elastic fibres are occasionally to be met with in the Human fæces, which present an appearance of transverse division (probably resulting from incipient decomposition) closely resembling that which is normal in the ligamentum nuchæ of the Giraffe. So distinct, indeed, does the transverse division then become, that these fibres, when peculiarly abundant (as they are in the fæces of persons who have for some time been living upon mutton-chops, and have not put aside the segment of the aorta which each chop includes), have actually been mistaken for a confervoid growth in the fæces.

§ Rawitz, "Ueber die Einfachen Nahrungsmittel," Breslau, 1846; and the Analysis of Wehsarg and Ihring's Inaugural Theses in "Brit. and For. Med.-Chir. Rev.," vol. xiv. p. 528.

‖ Crystals of this salt sometimes occur in perfectly normal fæces; and in those cases in which the secreted fluids and the contents of the intestine readily undergo decomposition, as in typhus, cholera, and certain forms of dysentery, they are found in large numbers and of considerable size.

¶ Sixty to 250 grammes, Landois, "Lehrbuch," 1879, p. 333, with an average of 170 grammes.

was daily eliminated from the system by this channel.* Bischoff, Meyer, and Voit† have shown that a bread diet given to dogs causes a great increase in the amount of fæces; and Brücke‡ points out that the remarkably different effects observed by different persons who have submitted themselves to the so-called Banting's cure—some of whom complain of constipation, while others suffer from diarrhœa—is referable to the fact that whilst an exclusive meat diet is apt to cause diarrhœa, it always causes great diminution in the amount of fæces excreted; readily giving rise to the idea that constipation is present. The absolute quantity of solid matter discharged in the fæces in the 24 hours is about 460 grains, of which only 10 per cent. consists of undigested matter. Of the dry fæces, from 23 to 31·5 per cent. (the proportion being smaller with meat than with vegetable diet) consists of an inorganic ash; the composition of which is stated by Enderlin§ to be as follows:—

Alkaline chlorides and sulphates	1·367	Soluble in water.
Bibasic phosphate of soda	2·633	
Phosphates of lime and magnesia	80·372	Insoluble in water.
Phosphate of iron	2·090	
Sulphate of lime	4·530	
Silica	7·940	

The potash generally predominates greatly over the soda, but especially when the diet has chiefly consisted of muscular tissue. The reaction of the Fæces is usually acid, but sometimes neutral or alkaline. The study of the composition of the Organic portion of the Fæces is attended with so much difficulty and unpleasantness, that it has hitherto been scarcely prosecuted systematically. According to the inquiries of Dr. Marcet,‖ healthy Human excrements contain—1. A peculiar substance crystallizing in acicular, silky, four-sided prisms usually grouped into stellæ, not subject to spontaneous decomposition, possessing feeble affinities, fusing at about 203° F., containing Sulphur, and having a composition expressed by the formula $C_{78}H_{78}SO_2$: this he proposes to call Excretin.¶ In infants cholesterin may take the place of excretin in the Fæces.** 2. Stearic and Margaric Acids in combination with bases, especially lime and magnesia. 3. A colouring matter similar to that of blood and urine. 4. Small quantities of peptic and amylolytic ferments. And 5. An acid olive-coloured substance of a fatty nature, termed *Excretolic* acid, which is probably united in fæces with Excretin, or a basic substance closely allied to it. Dr. Austin Flint†† obtained a substance he termed Stercorin which results from the decomposition of Cholesterin, and Vanlair and Masius‡‡ isolated a colouring matter which they named Stercobilin.§§ The fæces of infants at the breast are yellow or greenish-yellow, the reaction always acid, the consistence from almost solid to that of a thin fluid, the smell never foul, but resembling that of acid milk. They invariably contain whitish fibrin-like flocculi, and under the microscope epithelial cells, fine hairs, and crystals of the fatty acids may be observed. Wegscheider‖‖ finds that

* Smith and Milner, "Syd. Soc. Year-Book," 1861, p. 83.
† "Zeitschrift für Biologie," Band v., vi., vii., viii. 1869–73.
‡ "Vorlesungen," 1874, p. 336.
§ "Ann. der Chem. und Pharm.," 1844. Porter in do., t. lxxi., and Fleischmann in Poggendorff's "Annalen," 1849.
‖ "Proceedings of the Royal Society," June 15, 1854, and March 12, 1857.
¶ See Hoffmann, p. 173. ** Marcet, "Journ. of Chem. Soc.," 1862.
†† "Physiology of Man," part ii. 1867, p. 399. ‡‡ "Centralblatt," 1871, p. 369.
§§ Jaffe, however ("Centralblatt," 1871, p. 465), regards it as identical with his urobilin.
‖‖ Wegscheider "Ueber die normale Verdauung bei Saüglinge," Berlin, 1875; and "Centralblatt," 1876, p. 47.

the albuminous substances contained in the milk are completely absorbed. The so-called Milk-detritus is not casein, but consists essentially of fat and intestinal epithelium. The fats are not completely absorbed, a part is discharged in the form of soap, a part as free fatty acids, and some perhaps in an unchanged condition. Urobilin and unchanged bilirubin are found, and in slight disorder of the bowels Biliverdin. The Cholesterin presents no peculiarity. Diastatic and pancreatic ferments are present in small quantities, but no pepsin.

134. Of the degree in which the Bile, as a whole, normally enters into the composition of the fæces, it is difficult to speak with precision. Its principal constituents can be easily recognised in the upper part of the small intestine; but the further we descend in the intestinal canal, the less of them do we meet with; and in the contents of the large intestine, and in the evacuated fæces, they are only to be discovered in small quantity. How far this result depends upon their removal from the alimentary canal by re-absorption, and how far upon the loss of their characteristic properties by decomposition, cannot be stated with certainty. According to Bischoff, jun., in the human subject about 45 grains of the biliary acids are daily discharged by the fæces; whilst, according to Voit's estimate, about 170 grains are secreted by the liver, consequently, about 125 grains must be either re-absorbed or destroyed in their course through the intestinal tube. From the experiments of Hoppe-Seyler, it would appear that in dogs whose bile chiefly contains taurocholic acid, this acid undergoes changes in passing through the alimentary canal which are identical with those produced by boiling with acids, or with alkalies, or which occur in the act of putrefaction, cholalic acid, dyslysin, and choloidinic acid being produced. On the other hand, in the fæces of those animals that, like the ox, secrete bile, of which glycocholic acid is the chief constituent, this acid being comparatively stable and scarcely destroyed even by putrefaction, may be found in considerable quantity. That the colouring matter of the fæces is in great part derived from the bile, is shown by their clayey colour when that secretion is not duly poured into the intestinal tube. And it is probable that the peculiar fatty substances usually present are products of the metamorphosis of its oleaginous and resinous matters. Cholesterin is constantly present.* The researches of Bidder and Schmidt upon the amount of *sulphur* in the fæces appear to show that not above one-eighth of the solid matter of the bile is normally excreted under this form. The indications of the presence of bile are especially distinct when the fæces have remained for only a short time in the large intestine, and when there has consequently been less time for its re-absorption. Meconium contains unaltered Bilirubin and Biliverdin, together with Glycocholic and Taurocholic acids.

135. Planer† examined the Gases developed in the alimentary canal of Dogs after different kinds of food, and in Man after death. The gas contained in the stomach consisted chiefly of air swallowed with the food, and was usually small in quantity. The Oxygen soon disappeared. In the small intestines, Carbonic Acid and Hydrogen are developed in nearly equal proportion, whether the diet be Animal or Vegetable. The appearance of these gases in the intestines is attributable to putrefactive fermentation, which is accompanied by the development of bacteria. In the conversion of starch and sugar into lactic and butyric acids there is an evolution of Carbonic Acid and Hydrogen: thus—one equivalent of Sugar $C_{12}H_{12}O_{12} = (C_8H_7O_3)\ HO + 4CO_2 + H_4$. It has been found that Hydrogen sulphide is constantly formed when the pancreatic

* Hoppe-Seyler, "Phys. Chem.," 1878, p. 336.

† Henle and Meissner's "Bericht für 1860," p. 274.

juice is allowed to act on Fibrin, but that no Hydrogen gas is disengaged unless a putrefactive ferment be present. In like manner neither Carbonic acid gas nor Hydrogen are evolved during the action of bile or of pancreatic juice on starch or fat, though both of these gases appear during their putrefaction.* In the large intestine, Carbonic Acid is chiefly present, but is mingled with Sulphuretted Hydrogen (after Animal diet), and if the food have been long retained in the body, with Carburetted Hydrogen (CH_4). In a dog which had been fed for 6 days on pure animal diet, and was killed 5 hours after a meal, he found—

	CO_2.	O.	N.	H.	SH.
In the Stomach . . .	25·20	6·12	68·68		
Small Intestine . . .	40·1	Traces	45·52	13·86	
Large Intestine . . .	74·19	0·63	23	1·41	0·77

In another dog fed with bread for 8 days, there was only sufficient gas for analysis in the small intestine; it consisted of—

CO_2.	O.	N.	H.
38·78	Traces	54·2	6·33

Ruge† has carefully examined the Gases of the large intestine in the Human subject after different kinds of food, and finds their composition tolerably constant,—Nitrogen Gas preponderating after the use of flesh, Hydrogen after milk, and Carburetted Hydrogen after Vegetable (Leguminous) diet. Though the gases were sometimes offensive, they never gave more than a trace of Sulphuretted Hydrogen. The following Table includes his chief results:—

Composition of the Gases of the Large Intestines after the use

	Of Milk, for		Of Vegetables (Leguminous), for					Of Animal Diet, for		
	1	2								
	48 hours.	72 hours.	48 hours.	72 hours.	96 hours.	2nd series of Experiments on same person.		24 hours.	48 hours.	72 hours.
CO_2	16·82	9·06	34·00	38·40	21·05	35·43	17·6	13·62	12·46	8·45
N	38·38	36·71	19·11	10·67	18·96	21·78	32·2	45·96	57·85	64·41
CH	0·92	0·00	44·55	49·36	55·94	42·79	50·2	37·41	27·58	26·45
H	43·88	54·22	2·34	1·67	4·03	0·00	0·0	3·01	2·09	0·69

In the absence of bacteria and the putrefactive process generally, no gases are found in the intestines of infants, but it appears shortly after birth, before any milk has been swallowed.‡

136. If we now cast a retrospective glance at the changes undergone by the several groups of substances employed as food in their passage through the alimentary canal, we shall find that—1. The *oleaginous compounds* are melted and finely divided in the stomach, and may, under certain conditions, even here undergo decomposition indicated by acid eructations. On entering the small intestine they are emulsified, and in part also decomposed by the action of the pancreatic juice and bile into fatty acids and glycerin. The

* Hüfner, Hoppe-Seyler's "Phys. Chem.," 1878, p. 329.

† "Beiträge zur Kenntniss der Darm-gase, Sitzungsbericht d. k. Akad. d. Wissenschaften" (Wien), 1862, p. 729.

‡ Breslau, "Monatschrift f. Gebürts-kunde," Band xxv. p. 238.

glycerin, though not further acted upon by the pancreatic juice, yet in the lower parts of the intestine and under the influence of putrefactive ferments in an alkaline solution breaks up into succinic and other fatty acids with the evolution of H and CO_2 gases. When taken in moderate quantities the fats are almost entirely absorbed before reaching the large intestine, though a small quantity of soaps of lime in combination with stearic, palmitic, and oleic acids, may generally be obtained from the fæces. If taken in excess the fats are discharged unchanged. 2. The *Carbohydrates* are converted into dextrin and a peculiar form of sugar, first by the saliva, secondly by the pancreatic juice, and thirdly by the succus entericus, and the sugar thus formed is quickly absorbed, or if in excess, may under the influence of bacteria and the putrefactive ferments yield lactic and subsequently butyric acid. Starch may, indeed, undergo all these changes in the mere act of putrefaction without the presence of the pancreatic juice. If, however, a large quantity of starch be eaten raw, as in the form of apples or other vegetables, a considerable proportion passes off by the bowels unaltered, and this is seen even in the Herbivora which have very long and capacious alimentary tracts. Acetic acid is decomposed into CO_2 and CH_4, and Cellulose appears to undergo the same change. Malic and tartaric acids yield acetic acid and CO_2. 3. The albuminous compounds are in part absorbed directly into the blood in the stomach, but for the most part undergo conversion in this cavity by the action of the gastric juice into acid-albumin and then into peptone. As the acid chyme traverses the duodenum it becomes mingled with the pancreatic and biliary secretions, the latter of which precipitates the peptones, whilst the pancreatic ferment is incapable of acting. Gradually, however, the acidity diminishes, and when from admixture of the bile, pancreatic juice, and succus entericus, the contents of the intestine have become alkaline, the pancreatic ferment re-dissolves and resumes its activity, which is then continued throughout the alimentary tract. Pancreatic peptones are now formed; leucin, tyrosin, asparaginic* acid and CO_2 appearing as secondary products. The final changes of the albuminous compounds in the lower part of the intestine by the action of the putrefactive ferments are Indol, Skatol, and Phenol with H_2H_2S. The gelatin-yielding tissues, especially when they have been previously cooked, appear to be readily dissolved and absorbed; as are also such substances as brain, and the tissue of glands generally (liver, pancreas, thymus, and kidney). Amongst the products that have been found when gelatin undergoes putrefactive decomposition with the pancreas are CO_2 in large quantity, NH_3 acetic, butyric, and baldrianic acids, and much leucin, but neither glycocol nor indol.† Lastly, *mineral compounds*, and the various fermented beverages, are but little altered in their passage through the alimentary canal, being directly taken up by the blood-vessels and lymphatics.

* Asparaginic acid $C_2H_3(NH_2)(COOH)_2$ is bibasic, and forms thin rectangular laminæ, or minute four-sided prisms. One part dissolves in 376 of water at 0° C. and in 18°·6 of boiling water. It is insoluble in alcohol, alkaline solutions rotate to the left, acid to the right. Weiske, Schrodt, and St. v. Dangel ("Zeit. f. Biologie," Band xv., 1879, p. 287) have shown that it possesses some nutritive value, and may, like gelatin, imperfectly supply the place of albumin. It is found in the seeds and buds of many plants.

† Nencki, "Ueber die Zeresetzung der Gelatin," &c., Bern, 1876.

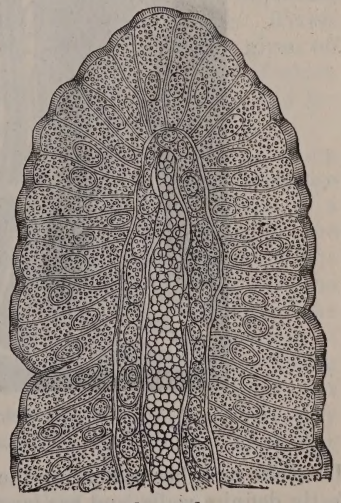
CHAPTER VI.

OF ABSORPTION AND SANGUIFICATION.

1. *Of Absorption from the Digestive Cavity.*

137. So long as the Alimentary matter remains in the Digestive cavity, however perfect may be its state of preparation, it is as far from being conducive to the nutrition of the system, as if it were in contact with the external surface. It is only when absorbed into the vessels, and carried by the circulating current through the very substance of the body, that it becomes capable of being appropriated by its various tissues and organs. In Man, as in nearly all Vertebrate animals, a set of vessels, first observed by Caspar Aselli in 1622, is interposed between the walls of the intestine and the sanguiferous system; for the purpose, as it would seem, of aiding in the taking-up of certain components of the nutritive matter, of which part at least are not in a state of perfect solution, and of preparing them for being introduced into the current of the blood. These are the *Absorbents* of the intestinal walls; of which those that are found, after the performance of the digestive process, to contain the white opalescent fluid known as 'chyle' are distinguished as *lacteals;* while the remainder, like the absorbents of the system generally, are known as *lymphatics.* The distinction is a purely artificial one; for the 'lacteals' are the 'lymphatics' of those parts of the intestinal walls which they supply, as is shown by the fact that, during the intervals of the digestive process, they contain a transparent fluid in all respects similar to the 'lymph' of other parts.—The Absorbents form a minute plexus beneath the mucous lining of the alimentary canal along its whole extent; but in the small intestine they enter the villi, at the extremities of which, indeed, they may be said to commence. Those only are entitled to the designation of 'lacteals' which originate from the intestinal canal below the point at which the biliary and pancreatic ducts pour their contents into it; for above that point, the fatty constituents of the alimentary matter are not in a state of sufficiently fine division to enter them; and the absorbed fluid is consequently pellucid, instead of possessing the milky aspect. Thus, then, we are to consider the *lacteal* portion of the Absorbent system to be that part of it which is specially adapted, by its prolongation into the villi, for the reception of an Oleaginous fluid; which we shall presently see to be taken up from the contents of the alimentary canal, and to be prepared for entrance into the absorbents, by the epithelium-cells at the radical extremities of those organs (§ 138).

Fig. 76.



c b a b c

Section of a Villus from the intestine of a rabbit: above (*a*) is the central canal, bounded on either side by the matrix (*b*), which again is covered by long columnar cells (*c*), containing a nucleus and granules. The outer border of these cells is seen to be straited.

138. The *Villi* are extensions of the mucous lining of the Intestinal canal, which thickly beset its surface from the pyloric orifice to the cæcum, that is, through the entire length of the Small Intestine, to which they are limited in Man. They have usually somewhat the form of the finger of a glove, being sometimes nearly cylindrical, sometimes rather conical, whilst they not unfrequently become flattened and extended at the base, so that two or more coalesce. Their length varies from 1-4th to 1-3rd of a line, or even more; and the broad flattened kinds are about 1-6th to 1-8th of a line in breadth.—In the upper part of the small intestine, where they are most numerous, it has been calculated by Krause that there are not less from 50 to 90 in a square line; and in the lower part, from 40 to 70 in the same area.—The details of their structure are of extreme interest in reference to the mechanism of absorption. If the plan pursued by Teichmann, that of injection, be adopted, the appearances presented are those shown in Figs. 77 and 78, taken from the beautiful plates which accompany his work on the Lymphatic System.* From these it appears that the lacteals commence either by a simple closed extremity, or by a loop, though in broad villi a network is sometimes visible.

Fig. 77.

A. Villi of Man, injected, showing the blood-vessels, and the lacteals.
B. Villus of a Sheep.

The tube or tubes occupying the centre of the villus appear to possess perfectly definite walls, and are larger than the numerous capillary blood-vessels which surround and are external to them. Their average diameter is about 1-800th or 1-1000th of an inch; but they present here and there slight dilatations and contractions, and at the base of the villus terminate in a network of lacteal vessels immediately subjacent to the Lieberkühnian follicles

* Ludwig Teichmann, "Das Saugader System," Leipzig, 1861.

(Fig. 78, *b*), termed by Teichmann, from the closeness of the meshes, the *Rete angustum*. This plexus communicates with another formed of larger vessels, which are supplied with valves, are more deeply situated in the submucous areolar tissue (Fig. 78, *c*); these constitute the so-called *Rete amplum*. Besides these plexuses, Auerbach* has more recently called attention to other plexuses of lymphatics, situated in and between the muscular coats of the intestines. In the longitudinal muscular layer one such plexus, and in the circular layer several may be found, to which he has applied the name of *interfascicular* lymphatic capillaries, all of which pour their contents into a median system of larger channels, possessing valves, and occupying the space between the circular and longitudinal muscular coats, which he has termed the *interlaminar plexus*. This last he considers represents the subserous or subperitoneal plexus of other observers, a layer which is only present at and in the immediate vicinity of the attachment of the mesentery. Some of the finest of these capillary lymphatics appear to have no other parietes than such as may be formed by the adhesion of a single layer of sinuously-contoured and tesselated epithelium-cells. In addition to the central lacteal, each villus is composed of a matrix of areolar tissue,† without any intermixture of elastic fibres, but having in its interstices numerous branched and inter-communicating cells containing nuclei, and frequently also fat-granules in their interior. The arrangement of the *blood-vessels*, according to Heller,‡ is that in man every villus contains an artery, which begins to lose itself in a capillary plexus, about the middle of the villus. The vein returning the blood begins at the point of the villus, and generally goes directly into the submucous tissue, without receiving any lateral branches. Both longitudinal and circular *muscular fibres* prolonged from the muscularis mucosæ§ are found in the villi. These surround the lacteal tubes, and their contraction, which has been frequently observed whilst absorption is going on, has an important influence on the propulsion of the fluids contained within the vessels. *Nerves* have been traced into the villi by Thanhoffer, who describes fibres given off from Meissner's plexus, ending in stellate granular cells, the processes of which penetrate the epithelial cells and are connected with their nuclei, and are partly also distributed to the muscular tissue and to the artery.‖

139. When the Villi are examined at such a period after a meal containing oleaginous matters as has sufficed for its partial digestion, their lacteals are seen to be turgid with chyle, the extremity of each being imbedded in a collection of globules presenting an opalescent appearance, and giving to the end of the villus a somewhat mulberry-like form. This appearance is due to the distension of the cylindrical epithelial cells *investing* the villi with the lacteal fluid. As it is a matter of much interest to examine and explain the mode in which absorption in this, its first stage, is effected, the attention of many observers has been directed to the structure of these columnar investing epithelial cells; and if the observations of v. Thanhoffer¶ be correct, our knowledge of the mode of absorption of various substances, and especially of those of an oleaginous nature, will be materially simplified. According

* Siebold and Kölliker, "Zeits. f. Wiss. Zool.," Band xv. 1865, p. 127.

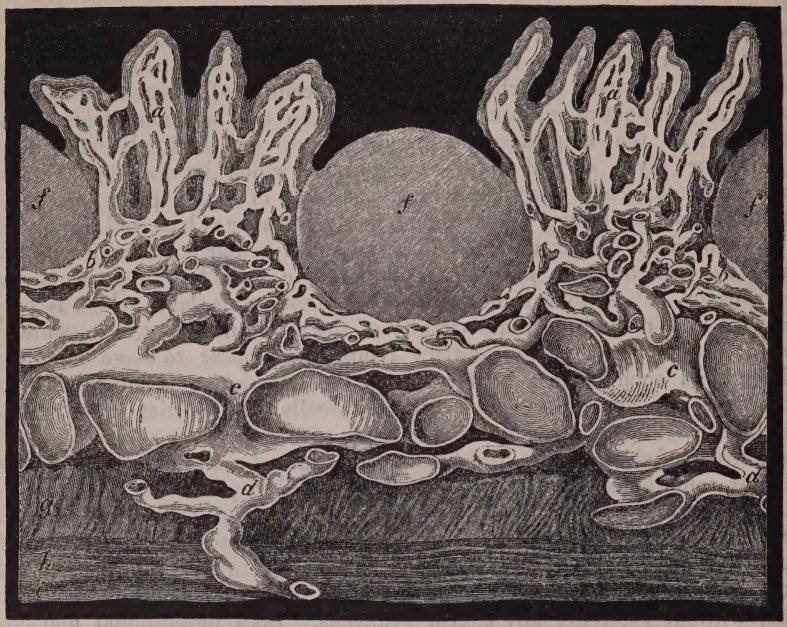
† Kölliker, "Manual of Human Histology," p. 325. ‡ Ludwig's "Arbeiten," Band vii.

§ H. Watney, "Proceed. Roy. Soc.," 1874, No. 152; L. v. Thanhoffer, Pflüger's "Archiv," Band viii. 1874, p. 441.

‖ Fortunatow in a recent communication states that he has been unable to discover these nerves (Pflüger's "Archiv," Band xiv. 1877, p. 285). They are, however, admitted by Landois, and various circumstances lend probability to their existence.

¶ v. Thanhoffer, Pflüger's "Archiv," 1874, p. 391.

FIG. 78.



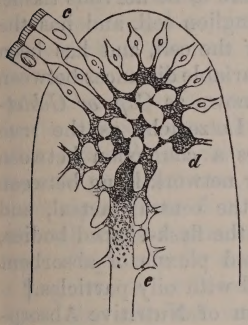
Perpendicular section through one of Peyer's patches in the lower part of the ileum of the Sheep. *a*. Lacteal vessels in the villi. *b*. The superficial layer of the lacteal vessels (rete angustum). *c*. The deep layer of the lacteals (rete amplum). *d*. Efferent vessels, provided with valves. *e*. Lieberkühn's glands. *f*. Peyer's glands. *g*. Circular muscular layer of the wall of the intestine. *h*. Longitudinal muscular layer. *i*. Peritoneal layer.

FIG. 79.

A perpendicular section through the wall of the Processus Vermiformis (Man). *a*. Lieberkühnian glands. *b*. Solitary follicle. *c*. Lacteal vessels, surrounding but not penetrating the follicles. At *d* are seen the larger efferent vessels, provided with valves.

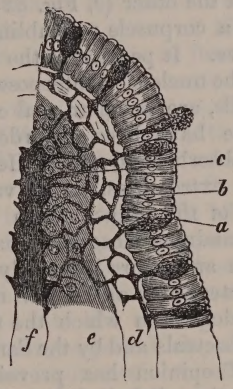
to this investigator,* the villi (*c*, Figs. 80 and 81, *a*, Fig. 82) are invested by a single layer of columnar cells, with a *broad free*, and a *narrower attached* extremity. The free extremity presents a thickened, bright, and highly refractile border surrounding the open mouth of the cell. The border varies in thickness and breadth in different cells, even of the same villus; and when the cells are examined from above, their margins seem to be continuous with each other, so that a kind of mosaic is formed. Immediately internal to the border (or perhaps projecting from the whole of the free surface of the cells)

Fig. 80.



Diagrammatic representation of the Origin of the Lacteals in a Villus, according to Funke:—*e*. Central lacteal; *d*. Connective-tissue corpuscles with communicating branches; *c*. Columnar epithelial cells, the attached extremities of which are directly contiguous with the connective-tissue corpuscles. After Funke.

Fig. 81.



Origin of the Lacteals according to Letzerich. The cells marked *a*, are cup or goblet cells, and are seen to be intercalated amongst the columnar epithelial cells, and to communicate with a delicate plexus, *b*, that opens at various points into the central lacteal, *c*, *f*; *d*, Layer of clear connective tissue; *e*, Connective tissue with numerous nuclei.

Fig. 82.

a. Body of Columnar cell from small intestine; *b*. Smooth border of cell; *c*. Protoplasmic processes; *d*. Connective-tissue processes; *e*. Nerve fibre penetrating the cell to join the nucleus; *g*, *f*. Ganglion cell (diagrammatic).

is a row of processes formed of the protoplasmic contents of the cell, which in mammals are rod-like or vertically striated, but in frogs, especially when examined in winter, are ciliaform and perform vibratile movements, which are particularly distinctly seen if the surface of the intestine have been brushed over with bile, and after division of the spinal cord or dorsal nerves. The processes quickly disappear after death, being replaced by a globular swelling projecting from the mouth of the cell, occasioned by the imbibition of water. The cells of the large intestine possess no bright border.

* See Heidenhain in Moleschott's "Untersuchungen," Band iv. 1858, p. 251; and Brücke in id. Band viii. 1862, p. 495; and in "Denkschrift. d. k. Akad. d. Wiss. zu Wien," Band vi. p. 105. Also Verson in Stricker's "Human and Comparative Histology," Syd. Soc. Transl. vol. i. 1870, p. 573. Ranvier, art. 'Epithelium' in the "Nouveau Dictionnaire de Médecin," t. iii. 1870. v. Thanhoffer, Pflüger's "Archiv," 1874, p. 391. These epithelial cells were described by MM. Gruby and Delafond ("Comptes Rendus," 1843, 1195) as possessing cilia on their free margin; but Kölliker, Funke, and more recently Schultze, considered this appearance as illusory, and produced by the thick membrane closing the free extremity of the cell being perforated by very delicate pores or canals, whilst after death it split up in such a manner as to *resemble* a bundle of cilia (Kölliker, "Mikroscop. Anat.," 1860, p. 329). Balogh, agreeing with Kölliker as to the lines in question being canals, differed from him in believing them to be not pre-existent, but merely the indications of the passages made by the molecules of fat in penetrating the delicate tissue occluding the mouth of the cell (Moleschott's "Unters.," Band vii. 1861, p. 556). Brettauer and Steinach, on

The *contents* of the cells during fasting are a mass of clear protoplasm, and a bright nucleus with nucleolus; but during digestion, especially of substances containing fat, the protoplasm becomes cloudy or granular, from the entrance of the molecules of oil into its substance; a process that is facilitated by the movement of the processes above described. The *attached extremity* runs out into two kinds of processes, one of which is continuous with stellate corpuscles (*d*, Fig. 80), forming a lymph canalicular system in the connective tissue matrix of the villus, which opens into the central lacteal vessel (*e*), thus affording a direct means of entrance for the fat molecules into the absorbent system, and explaining the occasional introduction of solid particles into the circulating current, whilst the other (*e*, Fig. 82) appears to be nervous tissue, since it is connected with a corpuscle resembling a ganglion cell, and has the chemical relations of nerve. It penetrates the foot of the cell, and has been traced by Thanhoffer to the nucleus. Interposed at variable distances between the ordinary columnar cells, are peculiar oval cells, known as *Cup- or Goblet-cells* (Fig. 81, *a*). These have been regarded by Letzerich* as the true commencements of the absorbent system. He traces a connexion between their attached attenuated extremities, with a vascular network lying between the basement-membrane of the villus, which joins the central lacteal, and states that after a meal containing oleaginous material the flask-shaped bodies, or cup-cells, the delicate and more internally situated plexus of absorbent vessels, and the central lacteal may all be seen charged with oily particles.†

140. In regard to the degree in which the function of Nutritive Absorption is performed by the Lacteals and by the Sanguiferous system respectively, considerable difference of opinion has prevailed. When the Absorbent vessels were first discovered, and their functional importance was perceived, it was imagined that the introduction of alimentary fluid into the vascular system took place by them alone. Such an idea, however, would be altogether inconsistent with the facts of Comparative Anatomy;‡ and it is completely negatived by the results of experiment. Absorption is effected to a very considerable amount by the agency of the Blood-vessels, as is shown

whose observations the statements of Brücke, Heidenhain, and other later authors are founded (Brettauer and Steinach, "Sitzungsbericht d. k. Akad. d. wissen. zu Wien," 1857, Band xxiii. p. 303), maintained that the apparent cilia are prolongations of the cell-contents, the cells themselves terminating with a smooth circular margin. They described the columnar arrangement as broadest and most distinct in fasting animals, whilst in cells filled with fat it diminishes to one-half or one-third of its former breadth, and the striæ disappear, so that only a bright narrow rim or border is left. Lastly, Wiegandt is stated in Canstatt's "Jahresbericht" for 1862, p. 32, to view the cilia as merely the optical expression of striæ or wrinkles.

* Virchow's "Archiv," Band xxxix. 167, p. 435.

† These statements of Letzerich have met with much opposition. Lipsky ("Wiener Sitzungsber.," Band lv. p. 183), Erdmann ("Die Resorptionswege," &c.), and Sachs (Virchow's "Archiv," Band xxxix. p. 493), regard the cup cells as the results of manipulation, and deny their original existence altogether. Others, as Oeffinger (Reichert's "Archiv," 1867, p. 337), and Thanhoffer (op. cit.), whilst admitting their presence during life, believe they proceed from natural changes occurring in the ordinary epithelial cells, such as imbibition of water, &c. Others, again, as Schultze ("Archiv f. Mikroskop. Anat.," Band iii. pp. 145 and 204), and Theod. Eimer, in whose little pamphlet ("Die Becherzellen") the reader will find an interesting epitome of all the essays (thirty-seven in number) on this subject up to 1868, are of opinion that there is a real and primary difference between the columnar cells and the cup cells, and they regard the latter as *mucus-secreting organs*. Verson (op. cit.) leaves the question undecided. It is right to add that some observers believe that oleaginous particles enter the substance of the villus between the epithelial cells (Fortunatow, Pflüger's "Archiv," Band xiv. 1877, p. 285; and Herbert Watney, "Quart. Journ. of Mic. Sci." 1877, p.204). For the latest views see Klein and Noble, "Atlas of Histology," 1879, p. 16.

‡ See "Princ. of Comp. Phys.," chap. iv.

in the first place, by the readiness with which water and saline solutions and even alcohol are taken up from the parietes of the Stomach, and are carried into the general circulation. Thus in a case of extroversion of the bladder, observed by Mr. Erichsen,* in which the urinary secretion could be collected immediately on its passing from the kidney, when a solution of ferrocyanide of potassium was taken into the stomach, this salt was detected in the urine in one instance within 1 minute, and in three other instances within $2\frac{1}{2}$ minutes. In the interesting experiments of Dr. Bence Jones and Dr. Dupré,† the rapidity of absorption of certain salts from the stomach is shown to be very great, a few grains of lithium chloride given to a fasting guinea-pig diffusing itself through all the vascular textures, and even into the cartilage of the hip-joint, in the short space of 15 minutes, and permeating every part of the lens, even in old animals, in four hours. In like manner, from experiments on cataractous lenses in man, it appears that traces of quinine may be discovered in the lens in about $2\frac{1}{4}$ hours after its ingestion. In the analogous eperiments of Eulenberg‡ and of Colin,§ iodide of p otassium, when injected into the stomach, could be detected in the parotidean saliva in from 20 to 45 minutes, and when into the small intestine of a horse in so short a period as 6 minutes in the chyle. In all these cases, however, the stomach may be presumed to have been empty, and the vascular system in a state of aptitude for absorption; since the experiments were made either after a long fast, or at least four hours after a light meal. When, on the other hand, the salt was introduced into the stomach soon after the ingestion of alimentary substances, a much longer period elapsed before it could be detected in the urine; thus, when a substantial meal had been taken two hours previously, the interval was 12 minutes; when tea and bread-and-butter had been taken one hour previously, the interval was 14 minutes; a similar meal having been taken 24 minutes previously, the interval was 16 minutes; when only two minutes had passed since the conclusion of such a meal, the interval was 27 minutes; and when a solid meal had been concluded just before the introduction of the salt, the interval was 39 minutes.—These facts are of great importance, in showing the very marked influence which the state of the *stomach* exercises upon the absorption of matters introduced into it. Not less important, however, is the state of the *vascular system* in regard to turgescence or emptiness; for it was found by Magendie, that when he had injected a considerable quantity of water into the veins of a dog, poison was absorbed very slowly; whilst, if he relieved the distension by bleeding, there was speedy evidence of its entrance into the circulation. If a small quantity of a concentrated solution of any salt, even if this possess a high endosmotic equivalent, be introduced into the stomach or intestine, it undergoes so much dilution that it is rapidly absorbed into the blood, but if a very large quantity be ingested osmosis in the opposite direction takes place, and diarrhœa results.—The rapidity with which not only aqueous but alcoholic liquids introduced into the stomach may pass into the general circulation has been shown by the experiments of Dr. Percy,‖ who found that, when strong alcohol was injected into the stomach of dogs, the animals would sometimes fall insensible to the ground *immediately* upon the completion of the injection, their respiratory and

* "Medical Gazette," vol. xxxvi. p. 363.

† "Proceedings of the Roy. Soc.," vol. xiv. p. 220, and xv. p. 73.

‡ Hermann in "Medicin. Centralblatt," 1865, p. 529.

§ Canstatt's "Bericht," 1865, p. 104.

‖ "Experimental Inquiry concerning the Presence of Alcohol in the Ventricles of the Brain," p. 61.

cardiac movements ceasing within two minutes; and that on post-mortem examination in such cases, the stomach was nearly empty, whilst the blood was highly charged with alcohol; thus rendering it almost certain, that not merely the final destruction of nervous power, but the immediate loss of sensibility, was due to the action of alcoholized blood upon the nervous centres.—Finally, numerous experiments have been made by various physiologists, which have demonstrated that absorption of alimentary and other substances may take place from the walls of the Stomach; these substances having been prevented from passing into the intestine by a ligature around the pylorus. Now, as the Absorbent system does not present that peculiar arrangement in the coats of the stomach, which it does in those of the intestinal tube, there can be little doubt that the introduction of such substances into the system must be effected chiefly, if not entirely, through the medium of its sanguiferous capillaries.

141. That the Blood-vessels of the *Small Intestine* largely participate in the introduction of soluble alimentary matter into the system has been clearly proved by various observations upon the constitution of the blood of the Mesenteric veins; these having shown, that after the digestion of albuminous and farinaceous or saccharine substances, albuminose, dextrin, grape-sugar, and lactic acid, are detectible in that fluid, whose usual composition is greatly altered by the presence of these substances, as well as by the augmented proportion of water which it contains. Again, it has been found that even after complete obstruction to the entry of the chyle into the circulation by ligature of the thoracic ducts, the digestion and absorption of albumin still take place, as indicated by the continued well-being of the animal and the appearance of the usual amount of nitrogen in the urine.* Moreover, it is asserted by Bruch,† that so large a quantity of fat is absorbed into the blood-vessels, that the superficial capillary network sometimes presents an opalescent whiteness. We may consider the Sanguiferous vessels, then, as affording the usual channel by which a large part of the nutritive materials are introduced into the system; but these are not allowed to pass into the general current of the circulation, until they have been subjected to an important *assimilating* process, which it appears to be one great office of the Liver to perform, whereby they are rendered more fit for the purposes they are destined to serve in the economy. Of this we shall have presently to speak.—The absorbent power which the blood-vessels of the Alimentary canal possess, is not however limited to alimentary substances; for it is through them almost exclusively that soluble matters of every other description are received into the circulation. This, which may now be considered a well-established fact, was first clearly shown by MM. Tiedemann and Gmelin,‡ who mingled with the food of animals various substances, which, by their colour, odour, or chemical properties, might be easily detected in the fluids of the body: after some time the animal was examined; and the result was, that unequivocal traces of such substances were not unfrequently detected in the venous blood and in the urine, whilst it was only in a very few instances that any indication of them could be discovered in the chyle.

142. It is a very remarkable fact, which has recently been fully substantiated, that not merely soluble matters, but insoluble substances in a state of minute division, may find their way from the alimentary canal and

* Schmidt-Mulheim, "Archiv f. Anat. u. Phys., Phys. Abth.," Band i. p. 549.

† Siebold and Kölliker's "Zeitschrift," April, 1853.

‡ "Versuche über die Wege auf welchen Substanzen aus dem Magen und Darmkanal in Blut gelangen," Heidelberg, 1820.

from the serous cavities into the current of the circulation. Thus, it was found by Oesterlen,* that particles of finely-divided charcoal, introduced into the alimentary canal, could be distinguished in the blood of the mesenteric veins; and similar results were obtained by Eberhard, and by Mensonides and Donders,† not only with charcoal, but also with sulphur and even with starch, the latter substance being at once detectible in the blood by the iodine-test. Such substances enter the lacteal system either through or between the epithelial cells of the villi. In favour of the former view is the fact that the presence of psorosperms in the interior of these has been distinctly perceived by Klebs.‡ In like manner, Ludwig and others in the Physiological School of Leipsic§ have noticed the penetration of particles of colouring matters from the interior of the abdominal or thoracic cavities into the lymphatics of the central tendon of the diaphragm, and into those of the pleura respectively; Auspitz‖ describes a similar absorption of starch corpuscles from the *peritoneal* cavity, and it seems probable that this is effected through certain openings (*stomata*) first noticed by Oedmannson,¶ and since fully described by Klein and others, which occupy interspaces between the ordinary tesselated epithelium-cells lining the serous cavities. These openings, therefore, establish a direct communication between the serous cavities and the lymphatic vessels, and the cavities themselves may reasonably be regarded, in one sense, as merely colossal dilatations of the vessels, analogous to those large lymph sacs or reservoirs which are found in the frog, fish, and other animals.**

143. There seems to be no reason for doubting that the absorption of the various nutritive and alimentary materials takes place according to the ordinary rules of Osmosis; for on the one hand is the aliment always more or less perfectly reduced to the liquid state, the density of which is generally less than that of the blood, in consequence of the very copious discharge of aqueous fluid into the alimentary canal during the operation of digestion; and on the other is the blood or lymph in rapid movement, possessing a high specific gravity, at a temperature of 99° or 100° F.; whilst between them is the septum, of immense extent and great tenuity, formed by the mucous membrane, and the walls of the blood or lymph vessels: the tendency is, therefore, in accordance with the general principles of osmosis to favour the passage of the aliment from the intestinal tract towards the circulating fluids.

Absorption of Albuminous Compounds.—As regards such substances as albumin, gum, and gelatin, which belong to the "colloid" class of substances, and therefore transude with extreme difficulty, it appears at first sight difficult to explain how they pass through the intestinal mucous membrane.††

* Heller's "Archiv," 1847. † Nederlandsch, *Lancet*, Band iv.

‡ For further information on this point the reader is referred to Moleschott's "Untersuchungen," Band ii. p. 119; and "Wien. Med. Wochenschrift," 1854, p. 817. Hollander, "Quæstiones de Corp. solid. e tract. intest.," &c., Dorpat, 1856. Teichmann, "Das Saugader System," 1861, p. 106. Funke, "Lehrbuch," 1863, 4th edit., p. 362 *et seq.*; and Klebs, in "Arch. f. Path. Anat.," Band xvi. p. 188; and especially to Auspitz, Essay in the "Wien. Med. Jahrb.," N.F. 1871, p. 283, in which the history of the subject is fully given.

§ See the several papers by Ludwig, Schweigger-Siedel, Dogiel, and Dybkowsky in the "Verhand. d. Sachs. Gesell. d. Wiss.," 1866.

‖ "Wien. Med. Jahr.," N.F. 1871, p. 583. ¶ Virchow's "Archiv," Band xxviii. p. 361.

** See M. Jourdain, "Ann. des Sci. Nat.," 1867.

†† Mialhe ("Chimie appliquée à la Physiologie," 1856) broke the shell from the end of an egg, leaving the membrane intact, and immersed it in water. After 5 hours it had increased in weight upwards of 30 grains, and the membrane was tight and prominent. The water in which the egg had been immersed became alkaline from the exosmose of the salts, but no albumin had escaped. So Graham and Eckhard ("Beiträge," Band iii. pp. 51 and 85, 1862) state that in analogous experiments with solutions of gum no exosmosis of that substance occurred.

The experiments of Funke, however, show that the act of digestion essentially effects a conversion of the "colloid" group into the "crystalloid;" for that as soon as the albuminous substances introduced into the stomach have undergone the modification into peptones, they have acquired the power of traversing animal membranes with comparative facility. As the conditions for the absorption of these substances are alike present in the stomach and intestines, it is probable that this process takes place through the whole length of the alimentary tube, though chiefly in the intestine, as the presence of acids is unfavourable to its active performance; a view which receives support from the experiments of Busch* upon the woman with a duodenal fistula, in whom it was found that a considerable portion of the saccharine, and about one-third of the albuminous compounds taken as food, were absorbed before reaching the intestines. Funke† observed, also, that when solutions of peptone were introduced and secured by ligature in determinate lengths of the intestines of living rabbits, and permitted to remain for two, four, and six hours, the more concentrated the solution, the greater was the activity with which the absorption was accomplished in a given time; but that a remarkable difference occurred from what might have been anticipated, where a definite quantity of the solution of peptone was presented to double the extent of surface, very little more being then absorbed, or at least nothing like double the amount in the same time. He further found that the amount absorbed in the living animal by no means stands in direct relation to the duration of the experiment, the process taking place with far more energy during the first hour than subsequently; and the same facts were also observed in experiments upon the absorption of sugar made by Becker.‡ The peptones are absorbed by both the lacteals and the blood-vessels, but their absorption proceeds slowly as only small quantities can be obtained from the chyle and portal blood, and as they have to restore the waste of all albuminous compounds they are probably speedily reconverted into albumin. The presence of common salt enables even raw albumin to be absorbed to some extent. If great excess of albumen be ingested, it appears in the urine.

Absorption of Fats.—Fats and oils are absorbed from the intestinal canal chiefly in the form of emulsion, partly also in the form of soaps. A certain quantity only is taken up, but the amount increases with the time during which digestion is progressing. If an excess be ingested, it is discharged unaltered in the fæces. The absorption is chiefly effected in the small intestine, since under ordinary circumstances little is found in the cæcum or colon. No difficulty exists in accounting for the absorption of soaps, but the oils and neutral fats could not penetrate a membrane moistened with water, unless some special provision existed by which this difficulty could be overcome. This provision is found in the bile, for it has been shown by various observers that if the entrance of bile into the intestines be prevented, a far smaller proportion of fat is absorbed, whilst it is well known that the bile aids in the formation of a fine emulsion, and Wistinghausen and Steiner§ have shown that such an emulsion will pass far more readily than oil through a moist animal membrane under a given pressure. It is probable that each particle of oil becomes surrounded by a layer of bile, and then partly by capillarity,‖ partly

* "Archiv f. Path. Anat. und Physiologie," 1858, Band xiv. p. 140.

† "Physiologie," 4th edit., 1863, p. 357.

‡ "Zeitschrift f. wiss. Zoologie," 1854, t. v. p. 137 *et seq.*

§ See Wistinghausen, "Endosmotische Versuche," &c., Dissert. Inaug., Dorpat, 1851; and Steiner, Reichert and Dubois-Reymond's "Archiv," 1873, p. 137.

‖ The importance of bile in aiding capillary attraction is shown in an experiment made

by the mechanical pressure exerted by the intestinal walls,* and partly, perhaps, by the action of the protoplasmic rods and processes of the intestinal cells,† gains entrance into their interior, from whence it is forced onwards by the periodical contraction of the muscular tissue of the villi themselves.‡ That in the case of the solid fats they must be capable of becoming fluid at the temperature of the body, and of forming an emulsion before absorption can be effected, is shown by the experiment of Funke, who found that stearin, the melting-point of which is 63° C., was not absorbed when introduced into the intestines of animals. The size of the oil drops is of considerable importance; the yolk of egg, for instance, mingled with two or three times its weight of water, will traverse the mucous membrane of the intestines at 100° F. with ease at a low pressure; but M. Morin§ experienced much difficulty with milk on account of the comparatively large size of the droplets. Adult cats are capable of absorbing about 0·6 grammes of fat every hour for each kilogramme of their weight; young cats about 0·92 gramme; dogs about 0·465 gramme; and geese about 0·8 gramme. The fats are taken up by both the lacteals and the blood-vessels.

Absorption of Carbohydrates.—Starch being insoluble, is not absorbed in the small intestine. The grape-sugar into which it is converted by the action of the diastatic ferments of the salivary, pancreatic, and intestinal glands is, however, almost entirely taken up in this part of the alimentary tract, 96 per cent. disappearing in the course of two hours. Cane-sugar which is in part also converted into grape-sugar is absorbed by both the lacteal and the blood-vessels, though very small quantities can be obtained from any given specimen of the chyle or from the blood of the portal vein at any particular moment. If taken in such excess that the quantity absorbed into the blood amounts to 0·6 per cent. of the blood, it appears in the urine.

144. *Absorption in the Large Intestine.*—Under ordinary circumstances, with the absence of villi and the change in the arrangement of the lymphatic system, it is probable that little besides water is absorbed from the aliment in the cæcum and colon. Up to the ileo-cæcal valve the contents of the intestinal tube are usually fluid, but beyond this point their consistence increases by the withdrawal of water till they assume a semi-solid form. It is well known that the life of patients, in whom from disease the entrance of food into the stomach is difficult or impossible, may long be sustained by the administration of nutritive enemata. Leube‖ has investigated the process of absorption that takes place under these circumstances, and has shown that albuminous compounds, especially in the form of peptones, as when minced muscle and pancreas are introduced into the rectum, a considerable quantity is absorbed, indicated by the improvement in the general condition of the patient by the increase in the weight of the body, and in the amount of urea eliminated by the kidneys, and by the actual diminution in the weight of the mass of nutritive material placed in the bowel. The addition of common salt, and of fat, providing it does not exceed one-sixth of the total weight, facilitates the process of absorption. Eichhorst¶ found that peptones, muscle, casein, salified

by Wistinghausen, in which two glass tubes having a diameter of 0·825$^{mm.}$ were placed vertically in olive oil. The interior of one of the tubes was wetted with distilled water, and in this the oil rose by capillarity 1·75$^{mm.}$ The interior of the other was moistened with bile, and in it the oil rose 11$^{mm.}$, or nearly six times higher.

* Béclard, "Physiologie," 1862, p. 181. † Thanhoffer, op. cit. ‡ Brucke, Op. cit., p. 338.

§ "Mémoires de la Société de Geneve," 1854.

‖ Leube, "Sitzungsbericht d. Med. Phys. Soc. zu Erlangen," Dec. 5, 1871. See also Jessen "Centralblatt f. d. Med. Wiss.," 1878, p. 612.

¶ Pflüger's "Archiv," 1871, Band iv. p. 570.

egg albumin, and gelatin were absorbed to a greater or less extent when injected into the large intestine. But pure egg albumin and coagulated fibrin were not absorbed. Bauer* observed that whilst little or no albumin is absorbed from the large intestine even when it has been well whipped, a considerable quantity is taken up if a little common salt has been added to it. In Voit and Bauer's experiments on a dog† white of egg underwent little or no absorption *unless* a little common salt were added; serum, albumin, syntonin, and peptones were taken up in larger but still small quantities. The amount of oil absorbed was also small, and they were unable to maintain life for any very long period by means of injections.

2. *Absorption from the Body in general.*

145. The Mucous Membrane of the alimentary canal is by no means the only channel through which nutritive or other substances may be introduced into the circulating apparatus from external sources. The *Lymphatic* system is present in all animals which have a *lacteal* system; and the two, as already pointed out, evidently constitute one set of vessels. The Lymphatics, however, instead of commencing on the intestinal walls, are distributed through most of the vascular tissues of the body, and especially in the Skin; but their number bears no proportion whatever to the vascularity of the several tissues, or to the amount of interstitial change which these undergo; and it would rather seem to be related to the amount of Connective tissue interposed between the other constituents of the fabric. Thus, we find the Nervous centres entirely destitute of them, unless, indeed, they are represented by the lacunar spaces filled with nuclei, which have been described by Robin‡ and His§ as surrounding the capillaries; and they are very scanty in the substance of Muscles. After passing, like the lacteals, through a series of glandular bodies (the precise nature of which will be presently considered), they empty their contents into the same receptacle with the lacteals; and the mingled products of both pass into the Sanguiferous system.—We find in the Skin, also, a most copious distribution of capillary blood-vessels, the arrangement of which is by no means unlike that of the blood-vessels of the alimentary canal; and its surface is further extended by the elevations that form the sensory papillæ, which are in many points comparable to the intestinal villi, although their special function is so different.

146. In the lowest tribes of animals, and in the earliest condition of the higher, it would seem as if Absorption by the *external surface* is almost equally important to the maintenance of life, with that which takes place through the internal reflexion of it forming the walls of the Digestive cavity. In the adult condition of most of the higher animals, however, the special function of the intestinal tract is so much exalted as usually to supersede the necessity of any other supply; and the function of the cutaneous and pulmonary surfaces may be considered as rather that of exhalation than of absorption. We have a remarkable exception to this general statement, however, in the case of Frogs and other Batrachia, which are characterized by the softness of their skins and the thinness of their epidermic covering; for cutaneous absorption seems in them to be no less active than their cutaneous exhalation and respiration are well known to be. And even in the higher animals there

* "Sitz. d. k. Bayer. Akad.," 1868, Band ii. p. 511.
† "Zeits. f. Biologie," Band v. 1869, p. 536.
‡ Brown-Séquard's "Journal de la Physiol.," vol. ii. 1859, p. 537.
§ "Zeits. f. wiss. Zoologie," 1865, p. 127.

are peculiar conditions of the system in which the imbibition of fluid through these surfaces is performed with great activity, supplying what would otherwise be a most important deficiency. It may take place either through the direct application of fluid to the surface, or even through the medium of the atmosphere, in which a greater or less proportion of watery vapour is usually dissolved. This absorption occurs most vigorously when the system has been drained of its fluid, either by an excess of the excretions, or by a diminution of the regular supply.

147. It may be desirable to adduce some individual cases, which will set this function in a striking point of view; and those may be first noticed in which the Absorption took place through the contact of *liquids* with the skin. It is well known that shipwrecked sailors and others who are suffering from thirst, owing to the want of fresh water, find it greatly alleviated, or altogether relieved, by dipping their clothes into the sea and putting them on whilst still wet, or by frequently immersing their own bodies.*—In a case related by Dr. Currie, of a patient labouring under dysphagia in its most advanced stage (the introduction of any nutriment, whether solid or fluid, into the stomach having become perfectly impracticable), an attempt was made to prolong his existence by the administration of nutritive enemata, and by immersion of the body, night and morning, in a bath of milk and water. During the continuance of this plan, his weight, which had previously been rapidly diminishing, remained stationary, although the quantity of the excretions was increased. How much of the absorption, which must have been effected to replace the amount of excreted fluid, is to be attributed to the baths, and how much to the enemata, it is not easy to say; but it is important to remark that "the thirst, which was troublesome during the first days of the patient's abstinence, was abated, and, as he declared, removed by the tepid bath, in which he had the most grateful sensations." "It cannot be doubted," Dr. Currie observes, "that the discharge by stool and perspiration exceeded the weight of the clysters;" and the loss by the urinary excretion, which increased from 24 ozs. to 36 ozs. under this system, is only to be accounted for by the cutaneous absorption.†—Dr. S. Smith mentions that a man, who had lost nearly 3 lbs. by perspiration, during an hour and a quarter's labour, in a very hot atmosphere, regained 8 ozs. by immersion in a warm bath at 95°, for half an hour.‡—The experiments of Dr. Madden§ on his own person show that a positive increase usually takes place in the weight of the body during immersion in the warm bath, even though there is at the same time a continual loss of weight by pulmonary exhalation, and by transudation from the skin.‖ This increase was, in some instances, as much as 5 drachms in half an hour; whilst the loss of weight during the previous half hour had been $6\frac{1}{2}$ drachms: so that, if the same rate of loss were continued in the bath, the real gain by absorption must have been nearly an ounce and a half. Why this gain was much less than in the cases just alluded to, is at once accounted for by the fact that there was no deficiency, in the latter case, of the fluids naturally present in the body.

* See a collection of such cases in Dr. Madden's "Experimental Enquiry into the Physiology of Cutaneous Absorption," p. 47.

† "Medical Reports," vol. i. pp. 308–326.

‡ "Philosophy of Health," vol. ii. p. 396.

§ Op. cit. pp. 59–63.

‖ That part of the function of Cutaneous Transpiration, which consists in simple Exhalation, is of course completely checked by such immersion; but that which is the result of an actual Secreting process in the cutaneous glandulæ (chap. xiv. sect. 4) is increased by heat, even though this be accompanied with moisture.

148. There are certain phenomena, which, if accurately recorded, cannot be accounted-for in any other way than by admitting that, under particular circumstances, a considerable amount of water may be absorbed from the *vapour* of the atmosphere. The following are among the most satisfactory and circumstantial observations that have been adduced in support of this position:—Lining observed that his body on one occasion increased in weight, during two hours, to the amount of 8½ ozs.; allowance being made for the amount of fluid ingested during that time, and for the quantity passed off by the urine and by cutaneous transpiration.* Dr. Jurin affirms that he ascertained an increase of 18 oz. to have taken place during a night passed in a cool room, after a day's exercise and abstinence.† It is stated by Dr. Watson,‡ that a lad at Newmarket, having been almost starved, in order that he might be reduced to a proper weight for riding a match, was weighed at 9 A.M., and again at 10 A.M., and he was found to have gained nearly 30 oz. in weight in the course of this hour, though he had only drunk half a glass of wine in the interim. Nearly the whole of the increase must here be attributed to absorption of vapour from the atmosphere; probably, however, rather through the lungs than through the skin. If the possibility of such absorption be admitted, we are probably to attribute to it the chief part of the excess of watery fluid which cannot be otherwise accounted for, in the following instances:—Dr. Hill§ relates the case of a diabetic patient, who for five weeks passed 24 lbs. of urine every twenty-four hours; his ingesta during the same period amounted to 22 lbs. At the commencement of the disease, he weighed 145 lbs.; and when he died, 27 lbs. of loss had been sustained. The daily excess of the excretions over the fluid ingesta could not have been less than 4 lbs.; making 140 lbs. for the thirty-five days during which the complaint lasted. If from this we deduct the amount of diminution which the weight of the body sustained during the time, we still have 113 lbs. to be accounted for, which can only have entered the body from the atmosphere.—A case of ovarian dropsy has been recorded by Mr. Ford,‖ in which it was observed that the patient, during eighteen days, drank 692 ozs. or 43 pints of fluid, and that she discharged by urine and paracentesis 1298 ozs. or 91 pints, which leaves a balance of 606 ozs. or 38 pints to be similarly accounted for.¶

149. The capacity of the Skin to absorb saline or other substances in solution is comparatively small, for no trace of Iodine can be detected in morning urine, when a bath containing half an ounce of potassium iodide dissolved in 80 gallons of water has been taken after six hours' abstinence from food.** M. Willemin, and others,†† have demonstrated that the healthy skin is capable of absorbing not only water, but small portions of various substances soluble in water; the process of absorption varying under

* "Philosophical Transactions," 1743, p. 496.
† Klapp, "Inaug. Dissert.," p. 30, cited by Dr. Madden.
‡ "Chemical Essays," vol. iii. p. 100.
§ "Trans. of Med. Chirurg. Soc. of Edinb.," vol. ii.
‖ "Medical Communications," vol. ii. p. 130.

¶ In this case, however, as in others of a similar kind, something is to be allowed for the quantity of water contained in the solid food ingested; but this may be fairly considered not to exceed the quantity lost by pulmonary and cutaneous exhalation, and discharged in the fæcal evacuations.

** See Murray Thomson, "Edin. Med. Journ," 1862, p. 1017; and Parisot, "Archiv Gén. de Méd.," 1863, p. 376.

†† "Archiv Gén. de Méd.," 1863, pp. 5, 105, 325; Delore, Ibid., p. 376; Hoffmann, "Comptes Rendus," 1867, p. 722; Clemens, "Archiv f. wiss. Heilk.," Band iii. 1867, p. 211; Brémond, *Lancet*, 1870, i. 495.

different circumstances, and often taking place very slowly, but being favoured by a delicate skin, and by exhaustion, though it does not take place when the skin is actively perspiring from exercise. The occasional serious effects upon the urinary organs of the application of a blister, the poisonous action of solutions of strychine, nicotin and digitalin,* the tinging of the urine with madder, rhubarb, and turmeric after bathing in infusions of those substances,† and, lastly, the remarkable experiment of Schreger, who found on immersing the hind leg of a puppy for 24 hours in tepid milk, after having previously applied a bandage, that the lymphatics were full of milk, though the veins contained none, all show that the skin possesses distinct but feeble powers of absorption. Homolle,‡ whilst admitting that pure water is certainly absorbed, and that saline solutions and some organic mixtures are sometimes decomposed by the skin, apparently by that tissue exerting an elective affinity for one of the constituents, to the exclusion of the others, states that in many instances in which he remained for an hour or more at a time in baths containing 3 ozs. of cyanide or iodide of potassium, nitrate of potash, or chloride of ammonium, he was unable to discover any trace of those salts in the urine, nor did he perceive any physiological effect from the employment of baths in which 1 lb. of belladonna or of digitalis leaves had previously been infused. The absorption of solid bodies (rice starch) and of mercury can be effected by rubbing them strongly into the skin, and is materially facilitated by the addition of any oily substance.§ When absorption does take place, we should expect that the absorbed substances would be more readily discoverable in the absorbents than in the veins; for their imbibition takes place entirely according to ordinary physical laws, in conformity with which they pass most readily into the vessels which present the thinnest walls and the largest surface.‖

150. Our inferences with regard to the ordinary functions of the Lymphatic system, however, must be rather drawn from the nature of the fluid which it contains, and from the uses subsequently made of it, than from such experiments as the preceding. We shall presently see that there is a close correspondence in composition between the Chyle of the Lacteals and the Lymph of the Lymphatics; the chief difference being the presence of a considerable quantity of fatty matter in the former, and of a larger proportion of the assimilable substances (albumin and fibrin) which are equally characteristic of both (§§ 154, 155). The close resemblance between the contents of the Lymphatics and diluted Liquor Sanguinis seems to indicate that the former are chiefly derived from the fluid portion of the blood, which has transuded through the walls of the capillary vessels, and has permeated the tissues, giving up to them the materials required for their nutrition. And we shall presently see reason to believe that this transudation answers the additional purpose of subjecting the crude materials, which may have been taken up direct into the blood-vessels, to an elaborating or preparatory agency, such

* Chrzonsczewsky, "Berlin Klin. Wochenschrift," 1870.

† "Medical Communications," vol. ii. p. 130.

‡ 'De l'Absorption par la tégument externe,' "L'Union Médicale," 1853, p. 462 *et seq.* See also Reveil, "Recherches sur l'Osmose," 1865; Oré, "Gaz. Médicale," 1865, p. 731; Mougeot, "Revue Médicale," 1865, t. ii. p. 536.

§ Auspitz, Op. cit., p. 320.

‖ For much interesting information respecting the increased energy, rapidity, and certainty of action of various poisons introduced directly into the circulation by the hypodermic mode of injection, as compared with the effects of the same substances when administered by the stomach, see the 'Report of a Committee of the Medico-Chir. Soc.' in vol. v. of the "Transactions" of that Society.

as it seems to be the especial object of the Lacteal system to exert upon the nutritive substances which *it* serves to introduce into the circulation.—But it seems not impossible that there may be another source for the contents of the Lymphatics. We have already had to allude, on several occasions, to the disintegration which is continually taking place within the living body; whether as a result of the limited duration of the life of its component parts, or as a consequence of the decomposing action of Oxygen. Now the *death* of the tissues by no means involves their immediate and complete destruction; and there seems no more reason why an animal should not derive support from its own dead parts, than from the dead body of another individual. Whilst, therefore, the matter which has undergone too complete a disintegration to be again employed as nutrient material is carried off by the excreting processes, that portion which is capable of being again assimilated may be taken up by the Lymphatic system. If this be the case, we may say with Dr. Prout, that "a sort of digestion is carried on in all parts of the body."—It may be stated, then, as a general proposition, that the function of the Absorbent System is to take-up, and to convey back into the circulating apparatus in a state of higher elaboration, such substances as are capable of appropriation to the *nutritive* process; whether these substances be directly furnished by the external world, or be derived from the disintegration of the organism itself. We have seen that in the Lacteals the selecting power is such that these vessels are not disposed to convey into the system any substances but such as are destined for this purpose; and that readily diffusable matters are absorbed in preference by the mesenteric Blood-vessels. The case is different, however, with regard to the Lymphatics; for there is reason to believe that they are more disposed than the venous capillaries to the absorption of other soluble matters, especially when these are brought into relation with the skin, through which the Lymphatic vessels are very profusely distributed.

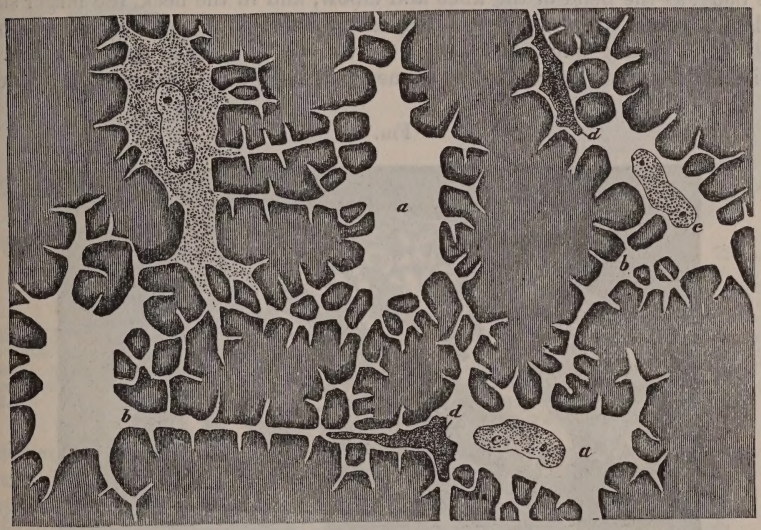
3. *Of the Elaboration of the Nutrient Materials.—Sanguification.*

151. The alimentary substances, taken up by the Blood-vessels and Absorbents, seem very far from being capable of immediate application to the nutrition of the body; for we find that they are not conveyed by any means directly into the circulating current, but that those which enter the Gastro-intestinal veins are submitted to the operation of the Liver, whilst those which are received into the Lacteals are subjected to a kind of glandular action within their own system; the newly-absorbed materials in both cases undergoing considerable changes, which tend to assimilate them to the components of the Blood.—The Lymphatic System* consists of an extensive network of vessels very generally distributed throughout the body, but present in remarkable abundance beneath the Skin and Mucous membranes. In regard to their origin it has been shown (§ 138) that in the villi the lymphatics end in processes like the finger of a glove, which, however, are probably connected laterally with irregular passages, containing stellate cells, through which the fluids absorbed gain entrance into their interior. In other parts of the body, as in fibrous and tendinous tissues, in membranes and fasciæ, a peculiar system of branched cavities is almost always visible when proper methods of preparation and observation are adopted. Each of the cavities contains a

* For an exhaustive account of the Anatomy of which, see v. Recklinghausen, Stricker's "Human and Comp. Histology," 1870, vol. i. pp. 297–346. See also Klein, "Anatomy of the Lymphatic System," 1873–74. I. Serous Membranes.

nucleated mass of protoplasm, which completely fills it; and both the cavities and their contents are in continuity with each other, so as to form a network which is now known under the name of *lymph-canalicular* system,* and the more or less branched cells contained in them are termed *lymphatic cells.*†

Fig. 83.



Cornea of Frog treated with lunar caustic.—*a*, canalicular system. In one place a branched flattened corneal corpuscle with its nucleus is seen; in two others are lacunæ of the canalicular system, containing nuclei *c*, of corneal corpuscles and *d*, migrating or wandering cells; *b*, branched channels, which connect the lacunæ of the canalicular system. Oc. 3, Obj. 9.

The large cavities and vessels with which the lymph-canaliculi communicate appear to be always lined, whilst their walls are sometimes exclusively formed by a delicate layer of flattened epithelial cells.‡ An external membrane is in the latter case gradually acquired, as the vessels become larger, on which again is superimposed a layer of dense connective-tissue, in which a few transverse muscular fibres may be distinguished. It is a peculiarity of the Lymphatics that they do not present the same smooth and regular contour, nor the same definite mode of branching, that is met with in the Blood-vessels; on the contrary, they run irregularly, and the walls of the vessels often present dilatations or reservoirs in their course, whilst the larger vessels formed by the reunion of several smaller ones, often again subdivide and reunite. The principal communication between the lymphatics and the blood-vessels is at the point where the great trunks empty themselves into the junction of the subclavian and jugular veins. It is not improbable, however, that in certain regions, as the cornea, the lymphatic canaliculi form channels by which the fluid parts of the blood, without its morphological constituents, can enter the

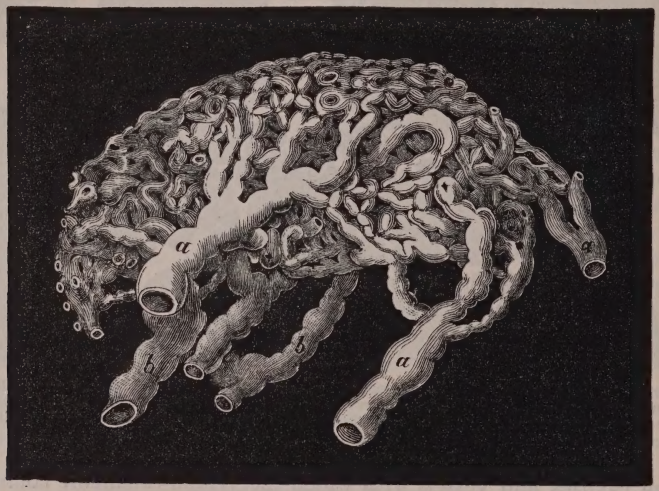
* Saftcanälchen of Recklinghausen.

† See Klein, in "Handbook for the Physiological Laboratory," 1873, p. 114; also Teichmann, "Das Saugader System;" Belajeff, "Journal de l'Anat.," t. iii. pp. 465 and 594. Ludwig, in the "Medizinischer Jahrbücher" of A. Duchek and A. Schauenstein, 1863, Heft. ix. pp. 35–77, Wien; Giannuzzi, "Ber. d. S. Gesells. zu Leipzig," Nov., 1855; Wywodzoff on the 'Lungs,' "Wien. Med. Jahrb.," Band xi. Heft iii. Genersich, in Ludwig's "Arbeiten," Band v. 1871, p. 53. Klein, "Quart. Journ. Mic. Sci.," 1877, p. 34.

‡ Auerbach, Kölliker's "Zeitschrift," Band xv. 1868, p. 172.

rootlets of the lymphatic system.* In many parts, especially in the central parts of the nervous system, the blood-vessels run in the interior of the lymphatic vessels, which form, as it were, an additional sheath to them, the place between the wall of the lymphatic vessel and that of the blood-vessel being occupied with fluid containing lymph corpuscles. At certain parts of the body, as the bend of the knee and elbow, and in the neck, the larger stems suddenly break up into a dense interlacing network of capillary vessels, most distinct in young subjects, forming a *rete mirabile*, as is shown in Fig. 84. This is surrounded by condensed connective tissue, and is penetrated by blood-

FIG. 84.



A section of a simple Rete Mirabile, viewed from the surface.—*a*, *a*, afferent vessels; *b*, *b*, efferent vessels only partially visible, from the popliteal space. (Man.)

vessels, constituting, so to speak, the first step towards the formation of a lymphatic gland. From this simple structure we can readily ascend through a series of gland-like organs, gradually increasing in complexity, composed of several of these little retia, arranged either continuously or in groups, until at length, by steps of easy transition, we arrive at the complex structure of the true lymphatic glands.†

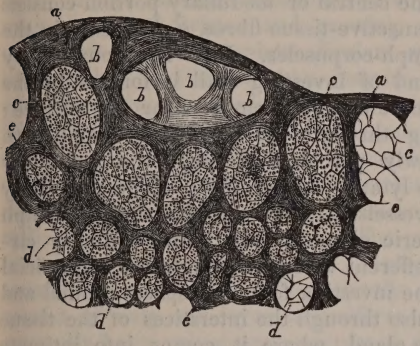
Every lymphatic gland is invested by a vascular sheath or capsule of condensed connective tissue (*a*, Fig. 86), which is continuous with the coats of the afferent and efferent vessels, sending inwards a number of thin lamellæ, so disposed and connected together as to constitute a tolerably regular alveolated framework pervading the gland, excepting usually near the centre. The septa thus formed contain in Man and many other animals, but especially in the Ruminants, numerous muscular fibre-cells, *d d*, Fig. 87. The alveoli are most distinct near the surface of the gland, *c c*, Fig. 85; towards the centre, in

* See Dr. T. A. Carter, "Journal of Anatomy and Physiology," 1870, vol. iv. p. 97.

† The details of the structure of the lymphatic glands have been most laboriously investigated and excellently described by His ("Untersuch. über den Bau der Peyerschen Drüsen," Leipzig, 1862), Kölliker ("Gewebelehre," 1866), Teichmann (Op. cit.), Frey ("Untersuch. üb. die Lymph-drüsen," Leipzig, 1861), v. Recklinghausen (Stricker's "Hum. and Comp. Hist.," Syd. Soc. Trans., 1870), and Krause ("Allgemeine und Mic. Anatomie," 1876).

consequence of the breaking up and irregular disposition of the septa, they are not very apparent. The centre of the gland is occupied by the medullary

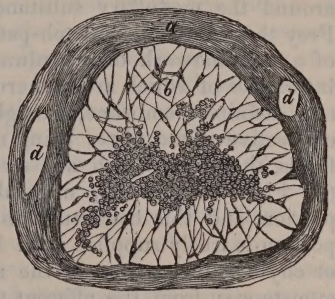
Fig. 85.



Section of *Lymphatic Gland*, showing, *a*, *a*, the fibrous tissue which forms its exterior; *b*, *b*, superficial vasa inferentia; *c*, *c*, larger alveoli, near the surface; *d*, *d*, smaller alveoli of the interior; *e*, *e*, fibrous walls of the alveoli.

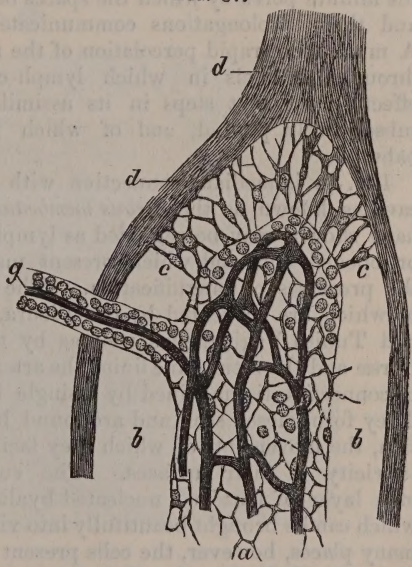
substance, varying considerably in amount in different instances, but always most abundant in childhood, and in the more deeply-seated glands. Its relation to the alveoli may best be understood by conceiving it to be a plastic substance, accumulated in mass at the centre, which sends out on all sides prolongations of the most irregular form and shape, which do nearly, but *not completely*, fill the alveoli. Spaces are consequently left between the septa which form the alveoli, and the processes of medullary substance partially filling them. These are termed the investing spaces (Frey) or lymphatic sinuses (His) of the follicle, and are represented by *b* in Figs. 86 and 87. They are traversed by irregular fibres, formed of nucleated cells with anastomosing prolongations, *c c*, Fig. 87. According to v. Recklinghausen,* they are lined by epithelial cells of a round polygonal form, and certainly contain numerous lymph-corpuscles. They are directly continuous with the afferent and efferent vessels, and may be filled with injection pro-

Fig. 86.



Simple Lymphatic Gland.—*a*. The capsule with sections of lymphatics. *d*, *d*, Coursing through it. *b*, Lacunar and intercommunicating passages, permeated by the lymph, and forming the superficial lymph-path of Frey. *c*, Nucleus or medullary portion of the gland, in the centre of which the section of a blood-vessel may be seen. The path pursued by the lymph through the medullary portion constitutes the deep or secondary lymph-path of Frey.

Fig. 87.



Portion of the Medullary substance of the Mesenteric Gland of an ox. The artery injected with Chromate of Lead × 300. *a*, Medullary substance with capillary network, fine reticulum of connective tissue, and a few lymph corpuscles; *b*, *b*, superficial lymph-path, traversed by a reticulum of nucleated cells (*c*, *c*) with numerous anastomosing prolongations. The lymph corpuscles have for the most part been removed with a camel-hair brush; *d*, *d*, Trabeculæ, composed almost exclusively of unstriped muscular tissue; *g*, a small medullary cord or bridge, containing a blood-vessel and numerous lymph corpuscles.

* See also Bizzozero, "Centralblatt," 1873, p. 110.

pelled from either of those sets of tubes; though, of course, on account of the valves, more readily through the former than the latter. The course which the lymph takes in traversing these somewhat lacunar spaces around the medullary substance contained within the alveoli is termed by Frey the superficial lymph-path. The central or medullary portion consists of a close network or reticulum of connective-tissue fibres, *a*, Fig. 87; in the interstices of which are numerous lymph-corpuscles. It is not bounded by any definite membrane, though a kind of investing wall is formed by the connective-tissue fibres being much more closely arranged near the surface; fluids, therefore, which are circulating through the superficial lymph-path (*b*) Figs. 86 and 87, may also slowly percolate through the medullary portion, and this constitutes the deep lymph-path of Frey. The medullary portion is freely supplied with blood-vessels. It thus appears that the lymph or chyle entering one of the mesenteric glands passes, under ordinary circumstances, from the afferent to the efferent vessels, through the superficial lymph-path, that is, chiefly through the investing follicular spaces around and between the alveoli: though partly also through the interstices of the tissue forming the medullary portion of the gland, where it comes into intimate relation with the blood-vessels, and takes up a certain proportion of lymph-corpuscles. When, however, the activity of the gland is at its height, as regards both the circulation of the blood and that of the lymph, as after food, the pressure of the increased quantity of the lymph effects the dilatation of the minute pores by which the spaces between the connective-tissue corpuscles and their prolongations communicate with the alveolar investing spaces. A much more rapid percolation of the newly-absorbed fluid is thus permitted through channels in which lymph-corpuscles are abundantly contained, effecting the first steps in its assimilation to the blood, into which it is subsequently poured, and of which it is obvious that it constitutes the pabulum.*

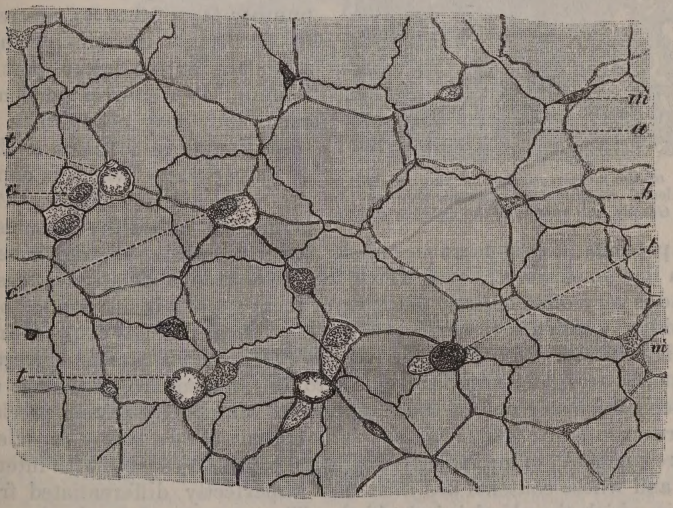
152. In immediate connection with the lymphatics are the large sacs or cavities known as the *Serous membranes*, which, as the researches of Klein† have shown, may be regarded as lymphatic glands that have been unravelled or opened out, and which present many points of interest in reference to the processes of sanguification. The serous membranes, typical examples of which are presented by the Pleura, Peritoneum, Pericardium, Arachnoid and Tunica Vaginalis, as well as by the Synovial membranes of joints and bursæ and the membrane lining the arteries and veins, are composed of a matrix of connective-tissue, lined by a single layer of cells termed the endothelium. They form closed sacs, and are found between parts that are subject to friction, the movements of which they facilitate by the extreme smoothness and lubricity of their surfaces. The endothelium for the most part consists of a layer of flattened nucleated hyaline cell-plates, the sinuous outlines of which can be brought beautifully into view by staining with nitrate of silver. In many places, however, the cells present a different character, being polyhedral, club-shaped, or even short-columnar with granular contents and ovoid nucleus, which is often constricted or divided into two. These germinating or young endothelial cells sometimes form projecting and pedunculated masses, and some of them, closely resembling lymph-corpuscles, may be seen either simply attached to the general surface, in the act of separating from it, or actually free in the cavity of the membrane. The matrix of the serous membranes,

* Oidtmann analysed a lymphatic gland from the inguinal region of an old woman and found it to consist of water 71·5, and solids 28·5, of which last 1·2 parts were salts.

† "The Anatomy of the Lymphatic System." I. The Serous Membranes. 1873.

best seen in such a part as the omentum, is composed of a homogeneous substance, in which are imbedded cells of various kinds. These, according to their form and arrangement, present (in the omentum of the rabbit, for example) two kinds of lymphangial structures. In one there are patches of more or less flattened branched cells lying in the lymph-canalicular system, multiplying by division and growing up into lymphoid cells which are also contained in the lymphcanalicular system. In the second kind there are patches and tracts, the matrix of which consists of a reticulum, containing in its meshes a variable number of lymphoid corpuscles. These patches are usually vascularized, but the former do not originally contain blood-vessels, though they subsequently become highly vascular; by coalescence they ultimately form large tracts. It is thus apparent that there is a considerable amount of adenoid tissue imbedded in, or rather forming the walls of, the serous membranes. The proper *lymphatics* of serous membranes form wide vessels, which partly accompany and sometimes invaginate or surround, and partly run independently of the blood-vessels, and their walls consist of only one layer of fusiform endothelial plates. The larger ones generally have valves and sacculated dilatations. The existence of stomata or openings on the surface of the serous membranes leading into lymphatic vessels, and forming therefore a communication between the cavity of the serous sac and the interior of the lymphatic vessels, has been clearly demonstrated. Dr. Klein distinguishes two kinds, the true and the false. The true,

FIG. 88.



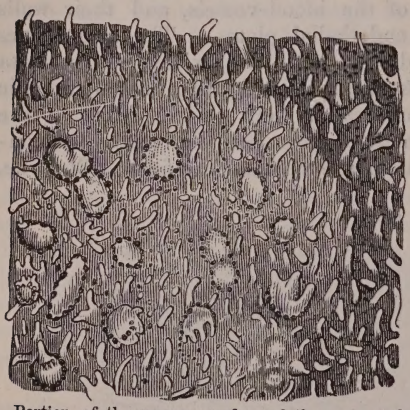
The large omentum of a young Rabbit, impregnated, without removal, with nitrate of silver.—*t*, holes in the membrane; *a*, contours of cells situated on the upper surface; *b*, contours of cells situated on the lower surface; *c*, *c*, small intercalated cells; *m*, masses of protoplasm stained with silver nitrate on the upper surface; *m'*, the same on the lower surface.

which are ciliated in the female frog and toad, are either the mouths of vertical lymphatic channels, which are lined by a special layer of polyhedral cells containing granular protoplasm, and lead into the lumen of a superficial lymphatic vessel, or they represent a discontinuity between the endothelial cells of the surface leading into a simple lymphatic sinus near the surface, lined on

one side only with epithelium. The false or pseudo-stomata are perpendicular processes which extend from the superficial cells of the cell-network of the matrix of certain nodules, and pass up between the endothelial cells of the surface.

153. The whole of the *Lacteal* and *Lymphatic* system, with the serous cavities in connection with it, may thus be looked upon as constituting one great *Assimilating Gland*, dispersed through the body at large; for it does not differ in any essential particular from what the Kidney or the Testis would be, if it were simply unravelled, and its convoluted tubuli spread through the entire system, yet still all discharging their secreted products by a common outlet. In the cold-blooded Vertebrata, the Absorbent system *appears* to attain a relatively greater development than it does in the higher classes; but the difference really lies in the greater extension, in the former, of those glandular elements which are more concentrated in the latter (See PRINC. OF COMP. PHYS., §§ 184—187).—Scattered through the whole length of the intestinal mucous membrane, from the Stomach to the Rectum, are certain peculiar bodies, which are known as *Peyer's Glands*. These may be either 'solitary' or 'agminated;' the former being very generally distributed throughout the intestinal canal, whilst the latter, in number from 20 to 80, are restricted to the small intestine, being most abundant at the lower part of the ileum. In whatever portion of the canal they may occur, they are always limited in situation to that part of its periphery which is opposite to the mesentery. Each 'Peyerian gland,' in a healthy mucous membrane, presents the appearance of a circular, white, slightly-raised spot, about a line in diameter, over which the membrane is usually less beset with villi, and is very often entirely destitute of them; and it is surrounded by a ring of openings, which are the orifices of a set of cæcal follicles disposed in a zone around it (Fig. 89). The 'Peyerian patches' (Figs. 89, 90) present aggregations of these spots, varying in number from 30 to 100 in a square centimeter (=·394 of an inch), but every one of their individual components having precisely the same structure as the solitary gland. This appears to be a sort of capsule, whose walls are composed of indistinctly-fibrillated connective tissue with interspersed nuclei, and whose contents are thus but imperfectly differentiated from the tissues in which the gland is imbedded. The contents of the glands are made-up of an adenoid or cytogenous tissue, the meshes of which contain lymph corpuscles, and fatty and albuminous molecules of various size; altogether presenting an appearance of being the seat of rapid changes of progressive metamorphosis. Each follicle is surrounded by a large lymphatic sinus,* beneath which is a close vascular network; capillary vessels pass freely into the midst of its contents, and then loop back, as shown in Fig. 90.† The

FIG. 89.

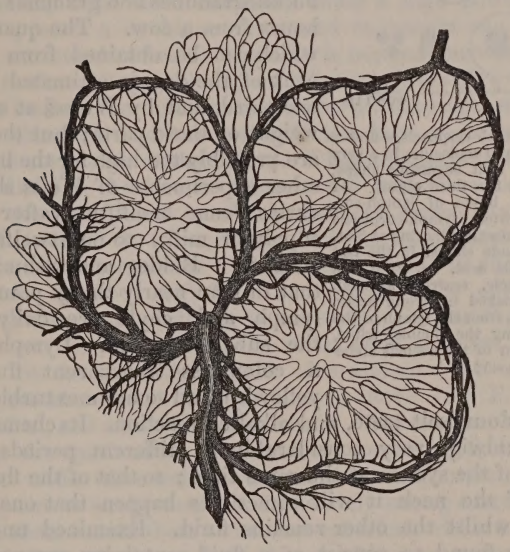


Portion of the mucous surface of the end of the Human Ileum, moderately magnified, showing the *Peyerian Glands*, the orifices of the follicles, and the villi.

* Klein, in "Handbook for the Physiological Laboratory," 1873, p. 125.
† Kölliker, "Mikroskopische Anatomie," Band ii. § 171.

researches of Teichmann* show that these bodies are never penetrated by any lacteal vessels, though their presence in the mucous membrane occasions considerable disturbance in the usual arrangement of the lacteal system. The figures on page 180 show clearly the relations which they hold to the surrounding vessels, together with the general structure of the small (Fig. 78) and large intestine (Fig. 79). In their course through the mesentery, the Lacteals pass into the bodies known as the *Mesenteric Glands*, which stand in the same relation to them that the *Absorbent Glands* of the body generally do to the Lymphatics.

Fig. 90.



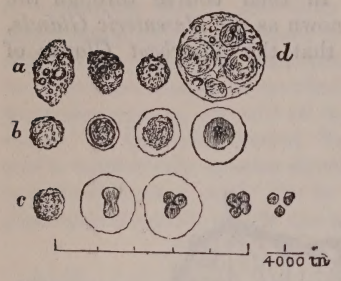
Horizontal Section through the middle plane of three *Peyerian Glands* in the *Rabbit*, showing the distribution of the blood-vessels in the interior.

154. *Composition and Properties of the Chyle and Lymph.*—The chief chemical difference between these fluids consists in the much smaller proportion of solid matter in the Lymph, and in the almost entire absence of fat, which is an important constituent of the Chyle. Lymph is found in the lymphatic

* Teichmann's investigations were chiefly made by means of injections; but His, who examined thin sections of the intestinal mucous membrane after merely washing them with water and a camel-hair brush ("Untersuch. über den Bau der Peyerischen Drüsen," Leipzig, 1868, p. 7), maintains the elaborate system of vessels described by Teichmann to be only splits or fissures in the membrane between the follicles, traversed by fibrous cords and bands, and containing blood-vessels. At the same time he agrees with the view that they serve as channels for the conduction of the chyle. He considers that the proper substance of the parietes of the follicles is continuous with that of the villi and subjacent portion of the mucous membrane; both consisting of a matrix of areolar tissue with nucleated cells imbedded in it, and of capillaries, the latter being sparingly distributed to the follicles, causing them to appear like clear spaces in fine sections. He applies the term adenoid tissue to the matrix of the follicles, and to the surrounding tissue of the intestinal mucous membrane. The Lieberkühnian Glands are imbedded in this adenoid substance, and immediately external to them is the muscular layer (Brücke) of the mucous membrane. He believes lastly, that the cells imbedded in the adenoid substance become blood-corpuscles.

system generally, and in the chyliferous vessels in the intervals of digestion; in the large serous cavities, as the peritoneum, pleura, and pericardium in the lymphatic ganglia, and in the interstices of the connective-tissues, and of the tendons and aponeuroses.* It may be obtained in large quantities by dissecting out and fixing a canula in the thoracic duct just before it discharges itself into the junction of the jugular and subclavian veins.† Lesser obtained by this means 300 cub. cent. of lymph from a dog in the course of four hours, and Colin no less than 95 kilogrammes 286 grammes in twenty-four hours from a cow. The quantity of lymph which can be obtained from the head and neck of the dog is estimated by Krause‡ at one-third, and by Weiss§ at one-fifth of the weight of those parts; but these proportions are probably too high for the body generally; other experiments of Weiss showing that it varies from one-fifth (after an abundant supply of milk) to one-twelfth of the total weight. Bidder and Schmidt‖ estimated that in man nearly thirty pounds of mingled lymph and chyle are daily poured into the subclavian vein. Lymph is, in general, a colourless transparent fluid, sometimes yellowish, and sometimes turbid or opalescent, having a faint odour, salt taste, and alkaline reaction. Its chemical characters, according to Ludwig, vary considerably at different periods, and even in different parts of the system at the same time; so that of the fluids taken from the two sides of the neck it will sometimes happen that one will coagulate spontaneously, whilst the other remains fluid. Examined under the microscope, lymph is found to consist of a fluid containing corpuscles of various kinds and of different size. Some of these are very minute oil globules, and are found to be most abundant after food; others are small masses of protoplasm which present some peculiarities, according to whether the lymph has been obtained from the vessels of a cold or of a warm-blooded animal. The lymph-corpuscles of the frog are spheroidal when quiescent, and may either remain so, or if carefully watched in a moist cell for some minutes may be found to throw out at ordinary temperatures amœboid processes, to flatten and extend themselves, and to again assume a spheroidal form, or owing to the mass of the cell following one or more of the processes, to execute slow movements of progression. It would hence appear that they have no cell-wall. After the lapse of a day or two, if the slide be again examined, some of the corpuscles appear spheroidal and unaltered; others are more or less irregular, the indications of their former amœboid movements; others present one or several nuclei, surrounded by granulations composed of oil; and others, lastly, have excrescences on their surface to which the term "sarcodic" has been applied, and which differ from the amœboid processes in being spherical,

FIG. 91.



a, Formation of lymph-corpuscle,—first a shapeless aggregation of molecules in a very finely-granular base, next acquiring shape, which is completed in the third object. At *d* is an endogenous brood of lymph-corpuscles. *b*, The perfect lymph-corpuscle acquiring a cell-wall, closely adhering at first, and distended and made clearer in the last object by dilute acetic acid. *c*. First, the perfect lymph-corpuscle, scarcely affected, after having been soaked in strong acetic acid; then pale cells, from the lymph of the thoracic duct, showing the double, triple, and quadruple division of the nucleus under the action of the same acid.

* Genersich, Ludwig's "Arbeiten," 1870.

† Colin, "Physiologie Comparée," t. ii. p. 101; and Lesser, Ludwig's "Arbeiten," 1872, p 94. ‡ "Zeits. f. rat. Med.," Band vii. p. 148. § Virchow's "Archiv," Band xxii.

‖ "Verdauungssäfte und Stoffwechsel," §§ 224, 285.

smooth, and homogeneous, and in remaining stationary when once emitted. Ranvier regards these bullæ as an indication of the death of the cell.* On the addition of iodized serum the corpuscles assume either a greenish-yellow or a port-wine colour, in the latter case owing to the presence of glycogen, and the nucleus and granulations quickly appear. A one per-cent. solution of picro-carminate of ammonia rapidly kills the corpuscles, brings their nuclei and granulations into view, and then stains them. A solution of carmine in ammonia of similar strength acts more slowly, but ultimately the nuclei become stained, and the same may be said of other colouring matters. Dilute solution of alcohol added to lymph proves immediately fatal to the corpuscles which assume the spheroidal form, emit sarcodic bullæ, and present well-defined nuclei; these when examined under a high power are found to be vesicular, to possess a double contour, and to contain one or more bright nucleoli. The nucleus is often so long that it becomes curved or twisted, or spirally coiled, so that the parts being in different planes give the impression of two or three nuclei. In different corpuscles all the stages of fission of the nuclei may be observed, and the act itself has been observed by Ranvier† in the lymphatic corpuscles of the axolotl. When the nucleus of any corpuscle has undergone division, the two or more nuclei formed seem to control the movements of the protoplasm by which they are severally surrounded, and to lead to the division of the mass, which, however, itself plays an active part, so as to form two new corpuscles. The entire process in one case occupied, at a temperature of about 62° F., three hours. The effect of heat on the corpuscles is distinctly exciting; it not only quickens their actions and renders them more energetic, but even when after removal from the body they appear to be dead, the application of moderate heat will cause their movements to recommence. At temperatures above 104° F. they soon die, becoming spherical, and exhibiting their nuclei. The presence of air or oxygen is requisite for the continuance of the movements after their removal from the body, even under favourable conditions of temperature and moisture, and oxygen appears to excite them. A moderately-strong current of electricity passed through them causes them to become spherical, whilst a strong current kills them and brings out the nucleus, though this may in part be due to the electrolytic action of the current. The lymph-corpuscles absorb blood-corpuscles or any minute foreign particles into their interior, as may easily be shown by injecting vermilion into the vessels before withdrawing the fluid. The corpuscles are not only able to seize upon and absorb neighbouring particles, but they can penetrate porous septa, as may be well seen by introducing a fragment of pith into the dorsal sac of a frog. In the course of twenty-four hours they will be found to have made their way in large numbers through the porous walls of the most superficial cells, and in less numbers into the deeper-lying cells. The latter die and speedily undergo fatty degeneration, accounting for the fatty deposit observed by Wagner and Middeldorf‡ in spongy bodies introduced into the serous cavities or into the tissues. The chief differences that are observable between the lymph-corpuscles of warm-blooded animals and those just mentioned are that they do not present amœboid movements at ordinary temperature, though at about 100° F. they are very active, the processes, however, being shorter. At 104° F. they suddenly assume the spherical form, and the nucleus and granulations appear. In their relations to oxygen, iodine, and other agents, they closely resemble the lymph-corpuscles of the frog.

* "Traité technique d'Histologie," 1878, p. 158. † Loc. cit., p. 161.

‡ Pitha and Billroth, "Handbuch der Chirurgie," 1865, vol. i. p. 338.

Ritter has counted 8200 corpuscles in one c. cm. of lymph taken from a dog. The number is always less in the peripherally situated than in the more central lymphatics. After being set free in the lymphatic glands the corpuscles are carried towards the vascular system in the larger lymphatics and in the thoracic duct, floating in a fluid which contains but little oxygen. The corpuscles then consequently become spherical and motionless, and have no tendency to escape. As soon, however, as they have entered the blood, they are brought into immediate relation with a highly oxygenized fluid and acquire activity, but being rapidly carried on have no tendency to stop or create an obstruction. But when from some morbid condition of the blood-vessels they accumulate at any point, they make their way out of the vessels, and the supply of oxygen being feeble, remain quiescent and form pus-cells. A knowledge of the physiological characters of the lymph-corpuscles is of great importance in medicine, since these bodies play an important part in many pathological conditions, and the results of treatment in the early stages of inflammation largely depend on the influence of the remedies employed on their movements and life. Chemically, the *lymph-corpuscles* consist of albumins and the soluble paraglobulin, and lecithin, nuclein, cerebrin, glycogen, cholesterin, and fat have been obtained from them. The *lymph plasma*, like that of the blood, contains fibrinogen, fibrino-plastic substance and ferment, probably derived from the lymph-corpuscles, and on standing forms a soft coagulum floating in lymph-serum. *Lymph-serum* contains alkali albuminate, precipitable by acids; serum albumin, coagulable by boiling; pepton, especially in the chyle; urea, leucin (0·1 – 0·2 per cent.: Wurtz); sugar and iron (2 per cent.: Colin). Some lymph taken from a peripheral lymphatic* contained about 97 per cent. of water, 2 of albumin, 0·2 of fibrin, and 0·8 of extractives. Another specimen taken from the thoracic duct yielded 94 per cent. of water, 4 of albumin, 1 of fibrin, and 1 of extractives. Chyle from a criminal contained 90·5 per cent. of water, albumin 7, fibrin a trace, fat 1, extractives and salts 1·5. Sugar, lactates, and a diastatic ferment (Grohé) have been observed in it. Hammarsten† found about 30–32 per cent. of gas in the lymph, of which nearly the whole was carbonic acid, the quantity of nitrogen being 1 per cent., whilst there was only a trace of oxygen.

155. In fasting animals, the composition of the *Chyle* appears to resemble very closely that of the Lymph, but during digestion its qualities sensibly alter. The characters of the *Chyle* drawn from the larger absorbent trunks, near their entrance into the Receptaculum chyli, are very different from those of the fluid first absorbed into the Lacteals; for during its passage through these vessels and the Mesenteric glands it undergoes important alterations, which gradually assimilate it to Blood. The chyle drawn from the lacteals that traverse the intestinal walls contains serum-albumin in a state of complete solution with paraglobulin and casein; but it is generally destitute of the power of coagulation, no Fibrin being present in it. The salts, also, are completely dissolved; but the oily matter presents itself in the form of globules of variable size.‡ It is generally supposed that the milky colour of the chyle is owing to these; but Mr. Gulliver has pointed out§ that it is really due

* For further analysis, see Appendix.

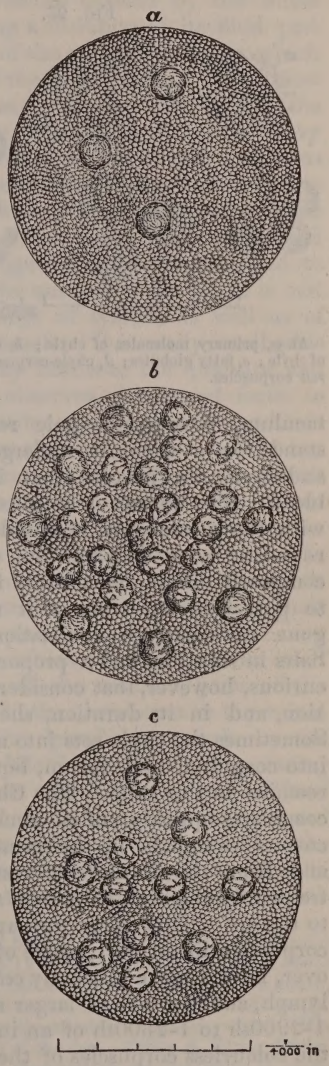
† Hammarsten, Ludwig's "Arbeiten," 1872, p. 121; Hensen, Ibid., Band xxxix.

‡ These oil globules are more abundant in the Chyle of Man and of the Carnivora than in that of the Herbivora; their diameter has been observed to vary from 1-25,000th to 1-2000th of an inch.

§ Gerber's "General Anatomy," Appendix, p. 88; and "Hewson's Works" (Sydenham Society Edition), Notes to pp. 82–88; and College Lectures in "Med. Times and Gazette,' 1863.

to an immense multitude of far more minute particles, which he describes as forming the *molecular base* of the chyle (*a*, Figs. 92, 93). These molecules are most abundant in rich, milky, opaque chyle; whilst in poorer chyle, which is semi-transparent, or opaline, the particles float thinly or separately in the transparent fluid, and often exhibit the vivid motions common to the most minute molecules of various substances. Such is their minuteness that, even with the best instruments, it is impossible to form an exact appreciation either of their form or their dimensions. They seem, however, to be generally spherical; and their diameter may be estimated at between 1-36,000th and 1-24,000th of an inch. Though remarkable for their unchangeableness, when subjected to the action of numerous reagents which quickly affect the proper Chyle-corpuscles, they are readily soluble in ether, the addition of which causes the whole molecular base instantly to disappear, not a particle of it remaining; whence it may be inferred that they consist of oily matter, which is partly in the condition of neutral fat and partly saponified. That they do not ordinarily tend to coalesce, is probably due to the coating of albumin which they obtain through their diffusion in an albuminous fluid; if, however, this be dissolved by acetic acid, or even when water is added, many of the molecules are lost sight of, and oil-drops appear in their place. The milky colour which the Serum of blood always exhibits in healthy subjects during the most active period of digestion is due to an admixture of this molecular base with the circulating fluid.

FIG. 92.

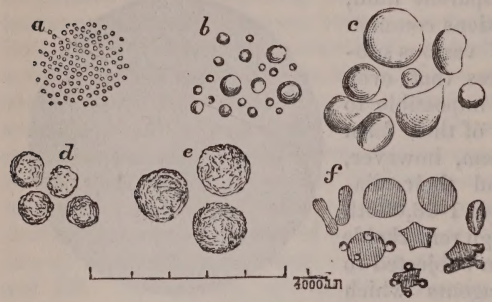


Molecular Base and Corpuscles of Chyle. At *a*, from a lacteal on the intestine; *b*, from a mesenteric gland; *c*, from the receptaculum chyli. From a man.

156. During the passage of the Chyle through the absorbents on the intestinal edge of the mesentery, towards the mesenteric glands, its character changes in several important particulars. The presence of Fibrin-factors begins to manifest itself by the slight coagulability of the fluid when withdrawn from the vessels; and a few chyle- or cytoid-corpuscles make their appearance; though these may occasionally be observed in the chyle from a lacteal on the wall of the intestine. The corpuscles are most abundant in the chyle of the mesenteric glands, and become less numerous again in the fluid of the thoracic duct (compare *a*, *b*, *c*, Fig. 92). The average diameter of these bodies is about 1-4600th of an inch. During digestion they are seen to be accompanied by much of the fatty molecular base of the chyle (*a*, Figs. 92, 93), some particles of which

have coalesced to form larger ones, surrounded by a thin layer of albumin (*b*, Fig. 93). Two, three, or more of the corpuscles may be sometimes seen enclosed within a common cell. The true Chyle-corpuscles appear to be at first in the condition of nuclei (*d*, Fig. 93), which take origin in the lymphatic glands of the mesentery; as these develop the cellular character becomes very distinct, and the nucleus may be plainly seen in the interior, especially after the addition of a little water or acetic acid. They exhibit the same changes of form as the colourless corpuscles of the blood, which are perhaps only the same bodies in a more advanced stage. The chyle drawn from the lacteals that intervene between the Mesenteric glands and the Receptaculum, possesses a pale reddish-yellow colour; and, when allowed to stand for a time, it undergoes a regular coagulation, separating into *clot* and *serum*, a process that is materially accelerated by the addition of blood. The former is a consistent gelatinous mass, which, when examined with the microscope, is found to include the corpuscles, each of them surrounded by a delicate film of oil; the fibrin of which it is principally composed differs remarkably from that of the Blood in its inferior tendency to putrefaction; whence it may be inferred that it has not yet undergone its complete vitalization. The serum contains the Albumin and Salts in solution, and a proportion of the Corpuscles suspended in it. It is curious, however, that considerable differences in the perfection of the coagulation, and in its duration, should present themselves in different experiments. Sometimes the chyle sets into a jelly-like mass, which, without any separation into coagulum and serum, liquefies again at the end of half an hour, and remains in this state. The Chyle from the Receptaculum and Thoracic duct coagulates quickly, often almost instantaneously; and few or none of the corpuscles remain in the serum. The fluid drawn from the Thoracic duct, and from the Absorbent vessels which empty their contents into it, is frequently observed to present a decided red tinge, which increases on exposure to the air. This tinge appears to be due to the presence of Red blood-corpuscles in an early stage of formation.* The ordinary corpuscles, moreover, have a more distinctly *cellular* character than have those of the chyle and lymph, and they are of larger size, their diameter usually ranging from about 1-2900th to 1-2600th of an inch: in these particulars they correspond with the colourless corpuscles of the Blood; as also in the change they exhibit on the action of acetic acid, which brings into view two, three, or four distinct central particles.

Fig. 93.



At *a*, primary molecules of chyle; *b*, secondary molecules of chyle; *c*, fatty globules; *d*, chyle-corpuscles; *e*, pale cells; *f*, red corpuscles.

157. The *movement of the fluids* taken up by the absorbent vessels seems to depend upon a combination of different agencies. The lower Vertebrata are provided with 'lymphatic hearts,'† or pulsatile cavities, by which important

* See Gulliver, "Med. Times and Gaz.," vol. ii. 1863, p. 449.

† See Wharton Jones on 'Lymphatic Heart of Eel,' "Proc. Roy. Soc.," Nos. 98 and 101, 1868; and John Priestley, "Journal of Physiology," vol. i. p. 1.

assistance is given to the onward flow; but no such aid is afforded in Man or in the Mammalia; yet it is obvious that a considerable *vis a tergo* must exist—since, if the thoracic duct be tied, it is speedily distended below the ligature, even to bursting. The main agent in effecting the movement in these animals appears to be the constant and considerable pressure exerted by the blood against the inner surface of the vessels, effecting a filtration of its fluid portions into the irregular cavities and interspaces of the connective tissue which are now believed to constitute the true origin of the Lymphatics. This view receives support from the experiments of Tomsa,* who has shown that the injection of serum into the vessels immediately after death, at the ordinary pressure of the blood, is followed by the filtration of a fluid closely analogous to lymph in its characters, which can readily be obtained from the lymphatic vessels. Abundant evidence exists to show that those circumstances which tend to increase the pressure in the capillaries, either by forcing more blood into any part,† or by preventing its return by ligature or pressure applied to the veins (provided that complete stoppage of the current of the blood is not produced), are followed by an increased discharge of lymph, as well as of lymph-corpuscles‡ from the larger absorbent vessels. It is easily intelligible that various other causes besides pressure may influence the quantity and quality of this fluid, which, as Milne-Edwards§ observes, is poured forth to *irrigate* the various organs of the body; for besides the important condition of the quality of the blood (with the effects of variations in which we are but imperfectly acquainted), differences in the thickness of the walls of the vessels and of the external pressure to which they are subjected, may to some extent be the causes of those differences in the nature of the transudate observed in Hydrocephalus, Ascites, and Hydrocele.‖ In the Lymphatics as well as in the Lacteals of the higher animals, the onward course of the contained fluids is probably aided by the contraction of the unstriped muscular tissue in their walls, assisted by the action of the valves; and to this perhaps we may attribute the emptiness of the absorbent system which usually presents itself some little time after death. Moreover, in all the movable parts of the body, material assistance is afforded (as it is to the circulation in the veins) by the occasional pressure exercised upon the lymphatic vessels by the muscles and other surrounding tissues; for while this pressure is operating it will tend to empty them of their contents, which are only permitted by the valves to pass in one direction; and when the pressure is relaxed they will be refilled from behind. In the lacteals, special agents for the propulsion of the chyle exist in the muscular fibres contained in the villi, which constitute so many minute force-pumps that are perhaps stimulated to

* The Serum used in Tomsa's experiments contained from 6·77 to 6·26 per cent. of solid residue, and that obtained from the Lymphatics from 6·12 to 4·36 per cent., which is about the proportion in ordinary lymph. Paschutin, however, has arrived at a different conclusion, and believes that variations in the arterial pressure have no influence on the flow of lymph. The secretion is increased, and its composition altered by the administration of curare. His experiments were made on the lymphatics of the fore leg of the dog. "Sitz. d. König, Sächs. Gesellsch. d. Wiss.," 1873, p. 95. For corroborative observations see Genersich in idem, 1870, and Emminghaus, Ludwig's "Arbeiten," 1873, Band viii. p. 51.

† As was effected by Mr. Robinson in his experiment recorded in the "Med.-Chir. Trans.," vol. xxvi. p. 51, when the aorta just above its division into the common iliacs, and also one of the renal arteries, were tied, and albumin immediately made its appearance in the urine, being as it were forced by the increased pressure in the remaining renal artery, through the delicate filter formed by the walls of the vessels in the Malpighian tufts.

‡ See Cohnheim, Virchow's "Archiv," 1867, Band xl. p. 1.

§ See his excellent chapter on Transudation in the "Leçons sur la Physiologie," vol. iv. 1859, pp. 391–446. ‖ See Hales's "Hæmastatics," pp. 118–119.

action (as suggested by Schiff) by the irritating properties of the bile. When the lacteal and lymphatic fluids have arrived at the thoracic duct, besides the forces already mentioned, their flow receives an additional impetus from a *vis a fronte* derived in part from the suction-power exerted by the rapid movement of the blood in the subclavian veins, the influence of which may readily be proved experimentally, and partly from the negative pressure exerted upon the walls of the duct during the period of inspiration, the opposing influence of expiration being neutralized by the valves.* Noll† found the pressure in the larger lymphatics of the neck in cats and dogs to be equal to that of a column of water varying from $\frac{1}{2}$ to $1\frac{1}{4}$ inch in height (10—30 mm.), but it is probably much higher in the smaller vessels. The rapidity of the current in the lymphatics of the neck is stated by Weiss to be about one-sixth of an inch per second.

That the *central nervous system* exercises considerable influence over the process of absorption is clearly shown by the experiments of Goltz.‡ In these, which were made upon frogs, rendered motionless by curare, the brain and spinal cord were removed in some instances, whilst in others they were left intact. In both sets of frogs fluid was injected into the dorsal lymph sac, and it was found that the fluid was rapidly carried off in those in which the brain and spinal cord were uninjured, whilst little or no absorption took place in those in which those organs had been removed. Nasse,§ who has also investigated this subject, found that irritation of sensory nerves caused increase in the flow of lymph. Excitation of the pneumogastric trunk, or of its central extremity when divided, augmented the flow. The influence of the nervous system is, however, in all probability *only indirect*, being due, in Goltz's experiments, to the circumstance that in the uninjured animals the circulation was maintained, whilst in those deprived of their nervous system the vessels of the body generally had lost their tone, and the blood accumulated in the veins of the abdomen and in other parts to such an extent indeed that little blood escaped even when the aorta was divided. In Nasse's experiments, again, the effects of the irritation of the sensory nerves was doubtless to cause contraction of the small vessels. The results of Krause's and Tomsa's experiments likewise lead to the conclusion that the influence of the nervous system is indirect, for whilst Tomsa found that irritation of the nerves proceeding to the testicle produced no alteration of the quantity, Krause obtained, both upon irritation of the mucous membrane of the mouth—that is to say, on irritation of the fifth pair of nerves—as well as on excitation of the portio dura, a considerable increase in the flow; the different effect in the two cases being clearly the result of the intermittent pressure of the *muscles* in the parts traversed by the lymphatics in the one instance, and the entire absence of muscles in the other.

158. Vascular or Ductless Glands.—There is reason to believe that the office performed by certain bodies connected with the Sanguiferous system, which possess the essential elements of the Glandular structure without any efferent ducts, is to restore to the circulating current any substances which they may withdraw from it; and there seems adequate ground, therefore, for the conclusion, that their action, whatever it may be, is subsidiary to the process of Sanguification,—being exercised, perhaps, upon that portion of the

* Dybkowsky, "Bericht. d. Sachs. Gesell.," 1866.

† Ludwig, "Physiologie," vol. ii. p. 581.

‡ Pflüger's "Archiv," Band v. p. 53. See also Bernstein, "Berliner klin. Wochens.," 1872, No. 28, and E. Heubel, Virchow's "Archiv," 1872, Band lvi. p. 248.

§ "Centralblatt," 1873, p. 155.

nutrient materials more especially, which did not traverse the Absorbent system when first introduced, but which was directly taken-up by the Blood-vessels. The organs in question are the Spleen, and the Thymus, Thyroid, and Supra-renal bodies. Of these the Spleen deserves especial notice, on account of its size and its obvious functional importance in the adult; the others appearing to minister more particularly to the requirements of the system at the earlier periods of life.

The principal points in the minute structure of the Spleen that may be regarded as established are that* it is essentially divisible into a lymphatic portion and a blood-vascular portion;† the former being represented by the Malpighian bodies and the sheaths of the arteries, the latter by the spleen-pulp. The whole is enclosed in a fibrous investment. These parts may be separately considered:—

I. The *fibrous coat* in Man is composed of white fibrous tissue, with an intermixture of yellow or elastic fibres, and a few fusiform non-striated muscular fibre-cells, especially at those points where the trabeculæ are given off from the capsule. The *trabecular tissue* consists of bands and threads of fibrous tissue, which arise from the inner surface of the fibrous envelope. The fibres form a network that extends through the entire organ, and they are connected with the sheaths of the vessels. They are almost entirely muscular in the dog and in those animals which have much muscular tissue in the external envelope. The spaces left by their intersection, which are by no means regular as to either form or size, are occupied by the splenic corpuscles and splenic parenchyma.

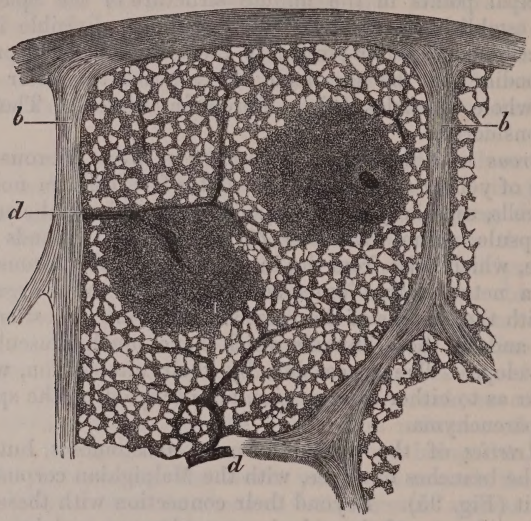
II. The *Arteries* of the Spleen form no anastomoses, but subdivide and ramify like the branches of a tree, with the Malpighian corpuscles attached to them as fruit (Fig. 95). Beyond their connection with these, however, they enter the general mass of the splenic parenchyma; and here each twig subdivides into a tuft of arterioles still more minute, which either pass directly into small veins (Billroth) or again subdivide into the true capillaries. At their entrance into the hilus of the organ, the arteries receive a sheath from the capsule composed of fibrillar connective tissue, with numerous elastic fibres, and a moderate proportion of muscle-cells. Where the arteries are not more than 1-75th to 1-125th of an inch in diameter the sheaths become much looser and converted into a cytogenous tissue.—The *Capillaries*, bounded only by their every thin walls, pass in very direction through the spleen-pulp, penetrating the general mass of the organ and the interior of the Malpighian corpuscles. In their further course the walls of the capillaries frequently disappear, and the blood, in passing from the minutest arteries to

* See Kölliker, "Cycl. of Anat. and Physiol.," vol. iv., Art. 'Spleen;' and "Mikroskop. Anat.," Band ii. §§ 183–189. Sanders, Goodsir's "Annals of Anat. and Physiol.," No. 1; and "Edin. Monthly Journal," March, 1852, p. 286. Wharton Jones, "Brit. and For. Med.-Chir. Review," vol. xi. p. 32. Huxley, "Quart. Journ. of Microscop. Sci.," vol. ii. p. 74; and Transl. of Kölliker's "Manual of Human Histology" (Sydenham Society), vol. ii. p. 144. Gray, "On the Structure and Use of the Spleen" (Astley-Cooper Prize Essay, 1854). Remak, Müller's "Archiv," 1852. Leydig, "Anatomische-Histologische Untersuchungen über Fische und Reptilien," 1853. Billroth, "Archiv für Path. Anat.," Band xx. p. 409 and 528; "Archiv f. Anat. und Physiolog.," 1857, p. 88; Crisp, "A Treatise on the Spleen," 1857. Kowalowsky, Virchow's "Archiv," 1861, p. 203. Schweigger-Siedel, Virchow's "Archiv," Band xxiii. p. 526. Stieda and Schweigger-Siedel, id., Band xxiv. p. 457; Peremeschko, "Sitzungsber. d. k. Akad. zu Wien," Band lv. and lvi., and Müller in "Gott. Nach.," 1862-1863; W. Müller, "Monograph on the Spleen," Leipsic, 1865, and Stricker's "Manual of Histology" (Syd. Soc. Transl.), vol. i. p. 348. Kyber, Max Schultzer's "Archiv," Band vi. p. 596. Olga Stoff and Sophie Hasse, "Centralblatt f. die Med. Wiss," 1872, p. 753. Klein, "Journ. of Mic. Sci.," 1875, p. 363.

† See Kyber, "Archiv f. Mic. Anat.," Band viii. p. 568.

the minutest veins, moves in great part through *lacunæ*, or mere channels in the pulp tissue. The *Veins* receive their blood from these lacunæ, and form at first a kind of rete mirabile, or close plexus of anastomosing vessels, from which the larger veins that accompany the arteries arise. The veins are unprovided with valves.

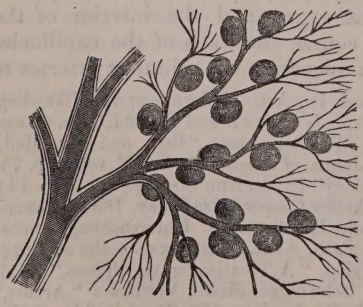
Fig. 94.



Section made at the periphery of the spleen in Man. At the upper part is the fibrous envelope sending off septa (*b*) into the interior of the organ. At its centre two Malpighian corpuscles are seen surrounded by the tissue of the pulp. The clear spaces correspond to the lacunæ of the serous network. *d*. Arterial ramifications.

III. The *Parenchyma* of the Spleen essentially consists of nuclei and cells in various stages of evolution, imbedded in a granular plasma (the periplast of Huxley); thus corresponding in every essential particular with the contents of the Peyerian glands (§ 153), and like them giving evidence of being in a state of rapid developmental change. Some of the nuclei are large and pale, and either spherical or flattened, others are smaller and elliptical. Kölliker and Klein have observed certain multinuclear flattened and branched cells, varying in size, and containing from four to ten or more nuclei; and similar bodies have been seen in the blood of the splenic vein. The peculiar *Splenic Corpuscles*, or 'Malpighian bodies of the Spleen,' are whitish spherical bodies, which may be regarded as lymph follicles. They are connected with the smaller arteries by short peduncles, like grapes with their fruit-stalks, or are sessile upon their sheaths (Figs. 94, 95). Their diameter usually varies between 1-3rd and 1-6th of a line; smaller bodies, however, are met with, which appear to be Malpighian corpuscles in an earlier stage of

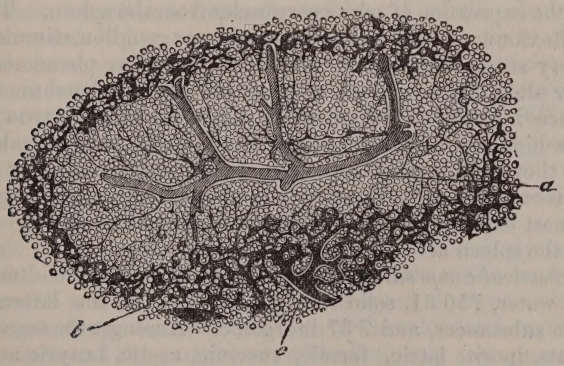
Fig. 95.



Branch of *Splenic Artery*, the ramifications of which are studded with *Malpighian corpuscles*.

evolution. The boundary of each is an indistinctly-fibrous membrane, partly formed by the metamorphosis of the external cells of the contained parenchyma, and partly derived from the fibrous coat of the artery to which it is attached. Its contents correspond, in every essential particular, with the parenchyma in which it is imbedded. The walls are covered with a plexus of capillaries, and branches from these traverse the interior, as in the case of the Peyerian glands. The number and size of the Malpighian corpuscles bear a remarkable relation to the general state of nutrition; being greatest in healthy well-fed animals, diminishing in those that have been ill-fed, whilst in those that have been starved they disappear altogether. Hence their existence in the Human species has been denied; the opportunity of examining subjects not reduced by previous abstinence, being one that comparatively seldom occurs. There is no doubt, however, of their normal presence in the spleen of Man, as in that of other Mammalia.—Diffused amidst the parenchyma of the spleen, but in very variable amount, are both *coloured* and colourless cells, some of which are unchanged blood-corpuscles, whilst others appear to be transitional forms between leucocytes and red blood-cells.* Others, again, seem to be blood-discs in various stages of retrograde metamorphosis; these gradually diminishing in size, and assuming a golden-yellow, brownish-red, or even blackish colour, or having the pigmentary matter crystallized in a rod-like form in their interior; or, again, breaking-up into detached pigment-granules. The colourless corpuscles are probably only nucleated buds of the general matrix, and after separation are carried away in the blood-current as lymphoid corpuscles.† Occasionally (though very rarely in the Human subject) little

Fig. 96.



Malpighian corpuscle from the spleen of the Hedgehog, with its vascular supply.—*b*, Splenic pulp, with the intermediary blood-passages; *c*, the rootlets of the veins.

clusters of from 1 to 20 degenerating blood-corpuscles are found, included in a vesicular envelope.‡ Some of these bodies are seen in the blood of the Splenic vein; and it has been hence concluded that they do not constitute normal elements of the Splenic parenchyma, but that they are either contained in its capillaries, or, if actually diffused through the pulp, are so as

* On this point see Freyer, "Inaug. Dissert." Königsberg, 1874; and E. Neumann, "Archiv f. Heilkunde," Band xv. p. 441.

† Klein, "Quart. Journ. Mic. Science," vol. xv. p. 367.

‡ See Gulliver, "Lond. and Edin. Phil. Mag.," 1842, p. 169, Fig. 2.

a result of an abnormal extravasation. The course of the blood through the spleen appears to be, as stated by Mr. Gray and W. Müller, that the splenic blood, in its passage from the arteries to the veins, ordinarily escapes from the walled vessels into indefinite channels traversed by connective tissue, so that its corpuscles become diffused through the parenchyma without any departure from its regular course; and it is a confirmation of this view, that the amount of *coloured* corpuscles in the spleen-pulp augments with the general turgescence of the vascular system, and diminishes with the poverty of the blood, so that, in animals reduced by ill-feeding, it disappears altogether.

IV. The *Lymphatics* of the Spleen are few and inconsiderable in Man; being less numerous than in other glandular organs, such as the liver and kidneys. In some animals, as the horse,* they are more abundant, and form two systems, one of which may be followed into the interior of the organ accompanying the larger arteries and veins, and investing the smaller vessels with a distinct sheath, between which and the parietes of the blood-vessel numerous lymph-corpuscles may be found; whilst the other forms a plexus in the trabeculæ.†

V. The *Nerves* distributed to the spleen in the dog are of two kinds, centripetal and centrifugal. Section of a centripetal nerve and stimulation of its proximal cut-surface induces strong contraction of the spleen and pain, whilst stimulation of the distal extremity is without effect. Stimulation of the distal cut-surface of a divided centrifugal nerve iuduces local contraction of the spleen in the part corresponding to the distribution of the nerve. Section of a centripetal nerve alone induces no change, but section of a centrifugal nerve causes local swelling, the part becoming blue. When all the splenic nerves are divided the spleen swells.‡ When they are stimulated by induction shocks the spleen contracts and the liver swells, results attributed by some to the expression of white corpuscles from the spleen. The immediate centre of reflexion appears to be the left semilunar ganglion, stimulation of which produces very strong contraction; but since the reflex phenomena are greatly weakened or altogether abolished after section of the splanchnic nerves before their entrance into the cœliac ganglion, it is clear that the true reflex centres must be at a higher point than the semilunar ganglia, and Bulgak§ has demonstrated that they are situated in the spinal cord in the region of the first four cervical vertebræ, and are connected with the left semilunar ganglion by fibres running almost exclusively in the left great splanchnic nerve. Nerve fibres influencing the spleen are also found in the vagus.

VI. The *chemical composition* of the Spleen was found by Oidtmann to be—in 1000 parts, water, 750·31, solid residue, 249·69; of the latter, 242·32 parts were organic substances, and 7·37 inorganic. Amongst the organic substances albumin, fats, inosit, lactic, formic, succinic, acetic, butyric and uric acids, with sarkin, xanthin, leucin, pigment, and much cholesterin have been distinguished. The most remarkable circumstances respecting the inorganic constituents are the large relative quantity of soda salts, and of oxide of iron.‖ The pulp has an acid reaction. From the observations of Mr. Dobson,¶ which have been corroborated by other observers, it appears that the Spleen

* See Tomsa, in "Sitz. d. k. Akad. zu Wien," Band xlviii., and Wedl, "Wien. Akad. Sitzber.," Band xiv. 1871, Abth. 1.

† See Kyber, in Max Schulte's "Archiv für Mikroscop. Anat.," Band. viii. 1872, p. 568.

‡ Drosdoff and Botschetschkaroff, "Centralblatt f. d. Med. Wiss.," 1876, p. 81.

§ Bulgak, "Centralblatt f. d. Med. Wiss," 1876, p. 577, and Virchow's "Archiv," 1877, Heft 2.

‖ v. Gorup-Besanez, "Physiolog. Chemie," 1872, p. 660.

¶ Dobson, "Lond. Med. and Phys. Journ.," Oct. 1820.

attains its maximum volume at the time that the process of chymification is at an end—namely, about five hours after food is taken; and that it is small and contains little blood seven hours later, when no food has been taken in the interval. The removal of this organ from the body has been performed, even in man, without serious effects; whilst in some instances in animals perfect regeneration has occurred, which is probably attributable to the hypertrophy of the little splenculi so often present in the immediate vicinity of the Spleen;* in others, enlargement of the lymphatic glands in various parts of the body, as the neck and axillæ, has been observed. Maggiorani† noticed a deficiency in the amount of iron contained in the blood-corpuscles; and in the dogs operated on by Dr. Dalton‡ an unnatural appetite and a ferocity of disposition were exhibited, which may perhaps be attributed to imperfect assimilation of the food they consumed. It has been found§ that such mutilated animals endure starvation for an unusually long period of time, and that they eliminate more uric acid than in health.

159. The *development*‖ of the spleen in man occurs at the close of the second month of intra-uterine life. It is entirely derived from the mesoblast, and makes its appearance in the fold of membrane, named the mesogastrium, which connects the intestinal canal to the spine, in close relation with the pancreas. It consists at first of small cells, but vessels and fibres develope in it during the third month, and it soon becomes highly vascular. The Malpighian corpuscles are not formed till near the time of birth.—The pulp-tissue, at an early period of its formation, closely corresponds with that of the Supra-renal and Thyroid bodies in their earliest stages of evolution; consisting of nuclei, nucleated vesicles, and a fine granular plasma. Peculiar amœbiform cells or protoplasmic bodies appear to be constantly present in the embryonal spleen, and in the splenic-pulp, but their function is unknown.¶ When the splenic vessels are being formed, many of the above-mentioned nuclei are surrounded by a quantity of fine, dark, circularly-arranged granules; and these appear to develop into nucleated vesicles, of which, when the splenic vein is formed, nearly the whole pulp is composed; the nuclei subsequently break-up into a mass of granules, which fill the cavities of the vesicles. Thus, during fœtal life we have evidence of a process of cell-growth and maturation, followed by cell-destruction, in the colourless parenchyma. The largest proportional size and the greatest functional activity of the Spleen seem to be exhibited during adolescence and the most vigorous period of adult life, its proportionate weight to the whole body being then as 1: 320 or 400. Tarchanoff** finds that stimulation of the central end of a divided vagus with a moderately-strong interrupted current induces in the course of a few minutes persistent contraction of the spleen and augmented blood pressure; stimulation of the peripheral end had scarcely any appreciable effect. Stimulation of the central extremity of the sciatic induced contraction of the spleen and increased blood pressure, though to a less extent, probably through irritation of the vaso motor centre. Stimulation of the medulla oblongata induces extremely well-marked contraction of the spleen, which at the same

* Phillipeaux and Mayer, "Comptes Rendus," 1861, p. 547.

† "Comptes Rendus," 1861, p. 319. ‡ "Human Physiology," 1871, p. 203.

§ Budge; Kühne.

‖ See Gray, 'On the Development of the Ductless Glands in the Chick,' in "Philosophical Transactions," 1852, p. 295; see also his Prize Essay.

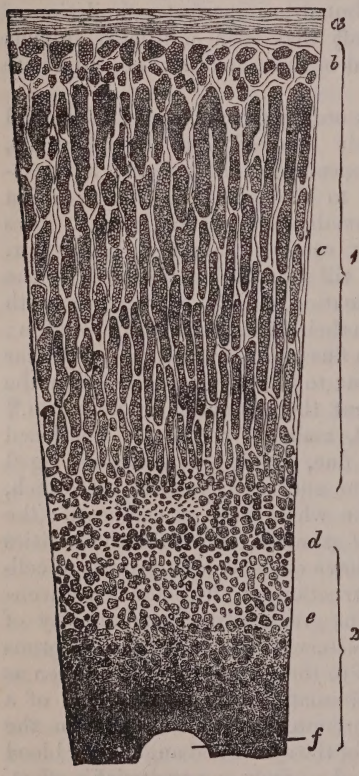
¶ Peremeschko, "Wien Acad. Sitzungsber.," 1867, Band lv. and lvi. Cohnheim, Virchow's "Archiv," Band xxxiii. p. 311.

** Tarchanoff, in Pflüger's "Archiv," Band viii. p. 97, 1874.

time changes its size and colour, these effects being only produced with uninjured splanchnics. The nerves of the spleen are large in Ruminants, but they contain much fibrous tissue.

160. The Adrenals (*Supra-Renal* bodies) in Man and most Mammalia present, like the kidneys, a division into cortical and medullary substances; the inner portion of the former having a remarkable dark-brown hue. The whole organ is invested by a fibrous envelope, from the inner surface of which processes are given off that dip into the cortical substance. The *cortical* substance has been divided by Arnold into three zones, named respectively the *Zona glomerulosa*, consisting of groups of cells imbedded in the meshes of a fibrous tissue; the *Zona fasciculata*, which forms the greater part of the cortex, and in which the groups of cells have a more columnar arrangement; and, lastly, the *Zona reticularis*, which is of a darker colour, and in which the columnar arrangement of cells is lost. The cells are everywhere polyhedral, finely granular, and frequently contain oil globules. The *medullary* substance is separated from the cortical by a layer of loose connective tissue, and is traversed in every direction by venous trunks. The stroma is delicate, and forms a reticulum, the meshes of which contain coarsely-granular cells. Some of these are branched. The supra-renal bodies are more highly supplied with nerves than any other gland-like structure in the body.* Kölliker counted no less than 33 branches proceeding to one of these bodies, derived from the sympathetic, pneumogastric, and phrenic nerves. These, after passing through the cortical, form a dense plexus in the medullary portion. In both parts, multicaudate ganglion cells are present. Holm, in the supra-renal bodies of oxen, found amongst other chemical constituents, inosit, with hypoxanthin, taurin, probably leucin, and an alkaline colouring matter.

FIG. 97.



Vertical section of Supra-renal Capsule of Man.—1, Cortex; 2, medulla. *a*, Capsule; *b*, layer of external cell-masses; *c*, columnar layer (*Zona fasciculata*); *d*, layer of the internal cell-masses; *e*, medullary substance; *f*, section of a vein.

161. Though Brown-Séquard† found that ablation of the Supra-renal Capsules was uniformly fatal, yet others‡ have shown that this effect is rather

* See Art. 'Supra-renal Capsule' in "Cyclop. of Anat. and Physiol.," vol. iv. Kölliker, "Mikroskop. Anat." Henle, "Handbuch der Anat.," Band ii. 1866, p. 561; also Gulliver's Appendix to Gerber's "Anat.," p. 103, and Figs. 266 and 267. Holm, Moleschott's "Untersuch.," 1867, Band x. p. 456. Arnold, Virchow's "Archiv," 1866; Grandry, Robin's "Journal de l'Anatomie," 1867; Eberth, in Stricker's "Human and Comp. Histology," vol. ii. 1872, p. 110.

† "Journ. de la Phys.," vol. i. 1858, p. 160.

‡ As Phillipeaux, "Comptes Rendus," 1856-57; Harley, "Med.-Chir. Rev.," 1858, vol. i.

attributable to hæmorrhage and the unavoidable injury to the nerves, and especially to the semilunar ganglia, attendant upon the operation, than, as Brown-Séquard believed, to the retention of some poisonous substance in the circulation, which it is the office of these bodies to remove. Since the year 1855 much importance has been attached to the study of the diseases of these organs, from the observation of Dr. Addison, that such cases are frequently associated with the deposition of pigment in the skin, causing it to assume a deep bronze colour. It has, however, been shown* that bronzing of the skin may be present and yet the supra-renal capsules be healthy; whilst cases† have been recorded in which disease was present in one or both of these organs, yet no bronzing of the skin occurred. Further inquiry is therefore requisite to determine whether the disease of the capsules and the discoloration of the skin really stand in the relation of cause and effect. According to Holm, a violet colour can be extracted from it, and Beaunis‡ states that it contains a peculiar organic substance which is reddened by iodine and rendered blue by iron perchloride.

162. In their *development* the Adrenals§ appear to be connected with the sympathetic ganglia.‖ They arise in the mesoblast before the seventh day of incubation, as two separate masses of blastema, situated between the upper end of the Wolffian bodies and the sides of the aorta; being totally independent (as concerns their development) of those bodies and of each other. The cortical and medullary portions have a distinct origin. From an early period their minute structure bears a close resemblance to that of the spleen, consisting of the same elements as that gland, excepting in the existence of more numerous dark granules, which give to the organ at a later period an opaque and darkly-granular texture; and their general history follows a very similar course: the Adrenals, however, acquiring their characteristic structure, and attaining their largest relative size, so early in fœtal life, as to surpass the Kidneys in dimension up to the tenth or twelfth week of Human embryonic development; though they afterwards diminish so much relatively to the Kidneys, as to possess in the adult condition only 1-28th part of their bulk.

163. The general structure of the *Thymus* Gland may be best understood from the simple form it presents, when it is first capable of being distinguished in the embryo. It is then solid,¶ but easily breaks down in the central part so as to form a single tube,** closed at *both* ends, and filled with granular matter; and its subsequent development consists in the growth of lateral shoots from this central axis. In its mature state it consists of an assemblage of glandular lobules, united together by connective tissue; and their cavities all communicate with a central mass, which some believe to be

p. 209; and Gratiolet, "Comptes Rendus," 1856. Dr. Creighton, in a paper read before the Royal Society in December, 1877, directs attention to the close histological similarity that exists between the cortical layer or zona glomerulosa of the Adrenals and those Graafian follicles, in which the ovum, after reaching a degree of ripeness, has shrivelled up and disappeared. The general intra-cortical mass he considers corresponds to another class of ovarian structures, the corpora lutea.

* Parkes, "Med. Times and Gaz.," 1858, p. 564.

† Kirkes, "Med. Times and Gaz.," 1857, p. 35; 1859, p. 30. See also Merkel in v. Ziemssen's "Cyclop. of Pract. Medicine," Amer. edit., vol. viii. 1878, p. 633.

‡ "Physiologie Humaine," 1876, p. 179.

§ See Balfour in the "Journ. of Anat.," vol. xi. 1877, p. 698.

‖ For a good account of the development of the supra-renal capsules see A. v. Brunn, in Schultze's "Archiv," Band viii. 1872, p. 618.

¶ Jendrassik, "Sitzungsbericht d. Wien Akad.," 1856, Band xxii. p. 75.

** The presence of a central cavity is denied by Dahms.

hollow (Figs. 98, 99). Each lobule is bounded externally by an indistinctly-fibrous membrane (Fig. 98, *a*), which sends prolongations (*b*) into its substance, that divide it into "acini" or gland-granules. Isolated gland-granules of the same kind are frequently to be met with on the main canal (Fig. 98, *c*).* The several follicles consist of a cortical and a

Fig. 98.

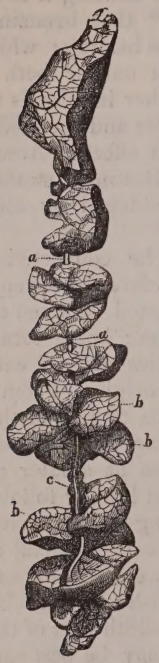


Fig. 99.

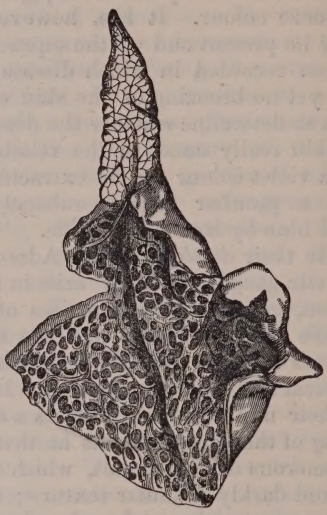


Fig. 98.—Portion of *Thymus* of *Calf*, unfolded.—*a*, Main canal; *b*, glandular lobules; *c*, isolated gland-granules seated on the main canal.

Fig. 99. — Section of *Human Thymus*, showing a cavity in the wide portion, and numerous orifices leading to its lobular cavities.

medullary portion, with a fine plexus of capillaries between them. The medullary parts of two neighbouring follicles are often united, so that this portion of the gland may perhaps be continuous throughout. Each follicle is composed of a reticulum of nucleated cells, and of cells. The reticular cells of the cortical portion have a disk-shaped nucleus nearly filling the cell, and give off long, fine-branching processes. The reticular cells of the medullary portion have one or two nuclei, present cell-bodies two or three times larger than the nucleus, and give off coarse, short processes. The medullary portion is also sometimes traversed by connective tissue trabeculæ. The free cells are of four kinds: small cells, resembling lymph-corpuscles; large granular cells of various sizes, many of which are attached by long processes to the trabeculæ and to the blood-vessels, and which contain one or two nuclei, and help to form (partly by a process of vacuolation) the concentric corpuscles of the thymus; giant cells, or multinuclear masses of protoplasm,† and

* See 'Note on the Minute Anatomy of the Thymus,' by Herbert Waling, "Proceed. Roy. Soc.," vol. xxvii. p. 369.

† See Prof. Kölliker's "Mikroskop. Anat.," § 208; Mr. Simon's "Physiological Essay on the Thymus Gland;" Peremeschko, "Zeits. f. wiss. Zool.," Band xxviii. p. 147. Mr. Gulliver's Lecture IV., "Med. Times and Gaz.," 1863, vol. ii. p. 503; and Klein in Stricker's "Manual of Histology" (Syd. Soc. Transl.), vol. i. p. 365. M. Dahm's "Etudes sur la Thymus," Thèse, Paris, 1877. "Afanassieff. Archiv f. mik. Anat.," 1877.

Hassall's concentric corpuscles, which, as Ecker has pointed out, may be either simple or compound. The simple corpuscles are spheroidal vesicles with a concentrically striated investment, and either contain a homogeneous substance exhibiting fatty lustre, or present granular material and a nucleus in their interior. The compound corpuscles are much larger bodies, and consist of several simple vesicles enclosed by a concentrically striated common investment. Both forms become more numerous as the gland advances to complete maturity, and are believed by Mr. Watney to be concerned in the formation of the blood-vessels and trabeculæ. The granular cells, giant cells, and concentric corpuscles are almost entirely confined to the cortical portion of the follicles. The *blood-vessels*, the tunica adventitia of which is formed by the reticulum, are of small size. They run in lines from the periphery of the follicle to the edge of the medullary portion, which they enclose in a ring and then penetrate, presenting at the same time a larger size. In fresh specimens colourless nucleated cells are seen, which contain granules and spherules of Hæmoglobin, and are either parts of the concentric corpuscles or are in close connection with them (Fig. 100). Between the vessels and attached to them

Fig. 100.

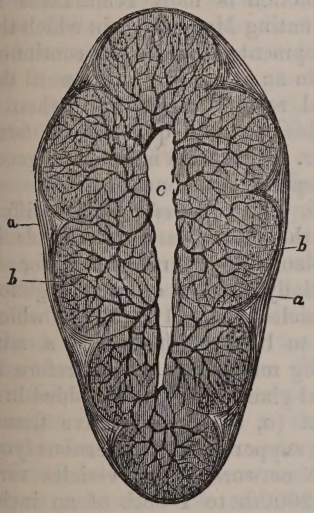


Fig. 101.

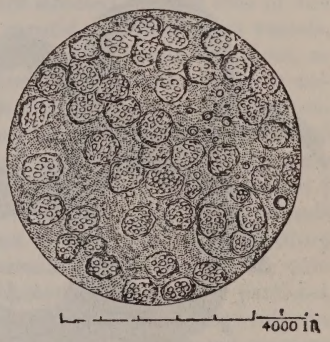


Fig. 100.—Transverse section through an injected lobule of the *Thymus* in a child.—*a*, Membranous investment of the lobule; *b*, membrane of the gland-granules; *c*, cavity of the lobule, from which the larger vessels branch-out.

Fig. 101.—Thymus-juice rich in corpuscles, with a few secondary molecules and the structureless minutely granular base.

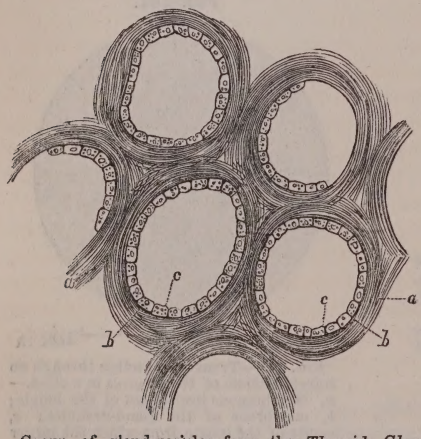
as well as to the connective tissue of the septa an exceedingly compact but very delicate network is extended, chiefly formed by the anastomosing branches of multipolar cells, in the interstices of which are numerous lymph-corpuscles; in addition a narrow meshed network may be observed, which is formed by the prolongations of the inter-follicular lymphatic vessels. The whole structure of the follicles resembles that of the Peyerian bodies.

164. The *lymphatics* of the interior of the follicles open into cavities lined by endothelium surrounding the follicles, which again communicate with elongated spaces imbedded in the trabeculæ and capsule of the gland. The chemical constituents of the *Thymus* are water, albumin, gelatin, sugar, fats, leucin, and sarkin, with xanthic, formic, acetic, succinic, and lactic acids, and the ordinary inorganic salts.* The expressed juice of the Thymus (Fig. 101)

* See Friedleben, in the "Journal de la Physiologie," 1859, p. 137; and v. Gorup-Besanez, "Phys. Chemie," 1862, p. 666.

in young and healthy animals possesses a creamy consistence and opacity due to the great abundance of corpuscles or free nuclei, identical in size, shape, and chemical characters with the corpuscles of the fluid of the lymphatic and mesenteric glands. The *nerves* are not very numerous, but were observed by Peremeschko partly to accompany the arteries, and in part to enter separately. Mr. Simon considers that they are mainly derived from the plexus which surrounds the first part of the subclavian artery, and which has its chief origin from the inferior and middle cervical ganglia. The greatest activity in the growth and development of this organ manifests itself, in the Human infant, soon after birth; and it is then, too, that its functional energy seems the highest. This rapid state of growth, however, soon subsides into one of less activity, which merely serves to keep up its proportion to the rest of the body; but its increase is continuous till the age of puberty is attained. From that time, during a variable number of years, it remains stationary in point of size; but, if the individual be adequately nourished, it gradually assumes the character of a mass of fat, by the development of the corpuscles of its interior into fat-cells, which secrete adipose matter for the blood. This change in its function is most remarkable in hybernating Mammals; in which the development of the organ continues, even in an increasing ratio, until the animal reaches adult age, when it includes a large quantity of fatty matter. The same is the case, generally speaking, among Reptiles.

Fig. 102.



Group of gland-vesicles from the *Thyroid Gland* of a child.—*a*, Connective tissue; *b*, membrane of the vesicles; *c*, epithelial cells.

165. The *Thyroid* body* differs from the other Vascular Glands in its elementary structures; for it essentially consists of an aggregation of vesicles† (Fig. 102, *b*, *b*), which seem to be furnished with a true limiting membrane, and therefore to be real gland-vesicles, imbedded in a stroma (*a*, *a*) of connective tissue, which supports a vast cavernous lymphatic network. The vesicles vary in diameter, in the Human subject from 1-2000th to 1-85th of an inch; and they contain an albuminoid plasma,‡ of either a faintly granular

* Good accounts of the Thyroid may be read in the following works:—Henle, "Handbuch der systematischen Anatomie des Menschen," 1866, vol. ii. pp. 535–541; Kölliker, "Handbuch der Gewebelehre," 5th edit., 1867, pp. 480–482; Verson, in Stricker's "Human and Comparative Histology" (Syd. Soc. Trans.), vol. i. pp. 370–372; Frey, "Das Mikroskop.," 4th edit., 1871, pp. 232 and 283; Baber, 'On the Lymphatics and Parenchyma of the Thyroid Gland of the Dog,' "Quart. Journ. Micros. Sci.," No. lxvii., for July, 1877, pp. 204–212, and "Philosoph. Trans.," 1876, vol. clxvi., part 2, p. 557 *et seqq*; Callender, "Proc. Roy. Soc.," vol. xvi. 1867, p. 25; Müller, "Jenaïsche Zeitschrift," 1871; Poincaré, "Journ. de l'Anat. et de la Physiol.," Sept. and Oct. 1875; Abstract in "Journ. of Anat. and Physiol." 1875, p. 451.

† These vesicles were formerly stated to be closed, but P. A. Boéchat ("Centralblatt," 1874, p. 84) has recently maintained, as the result of observations made upon healthy glands hardened in Picric Acid, subsequently placed in solution of gum, and finally in alcohol, that they intercommunicate freely.

‡ That the fluid does *not* contain true Albumin in solution, but some albuminous compounds, is indicated by the results of Dr. Beales's analysis ("Cyclop. of Anat. and Physiol.," vol. iv. p. 1106).

or of a somewhat oily aspect, which may be seen to exude from the epithelial cells (*c*, *c*) lining their interior. The vascular supply of the Thyroid body is extremely abundant; and, as in the preceding instances, the subdivisions of its arteries form a very minute capillary plexus upon the membrane of the vesicles. The *lymphatics* as described by Mr. Baber are very numerous, and are filled with a granular yellow material, which he supposes to be of a viscid consistence, and to be formed by a number of cells which may be termed parenchymatous; such cells originating in the inter-vesicular tissue external to the walls of the vesicles. The lymphatic spaces are lined by a layer of epithelium, which is often the only septum between the interior of the vesicles and the lymphatic spaces. The *nerves* are numerous, accompany the vessels, and are derived from the cervical parts of the sympathetic. They form close plexuses with interspersed ganglia.*—The Thyroid body originates on the third day in the Chick as an involution from the hypoblast of the throat opposite the point of origin of the second arterial arch. On the fourth day it forms a solid mass of cells, and on the fifth becoming independent of the epithelium of the throat, it presents a bilobed form, the two lateral masses being joined by a central portion or isthmus, with an outlying piece or pyramid of very variable form. The lateral lobes are situated on each side of the root of the neck, close to the separation of the carotid and subclavian vessels, and between the trachea and the branchial clefts, but quite independent, as far as regards their development, of either of those parts; their minute structure at an early period closely corresponds with that of the spleen and supra-renal glands. In Man the Thyroid body appears about the end of the second month of fœtal life, and then consists of tubes and vesicles, which subsequently become more and more defined, but no anastomoses have been observed.† Like the Supra-renal and Thymus, the Thyroid is of larger relative magnitude during intra-uterine existence and infancy than in after-life. The *Pituitary body* has the same essential structure as the vascular glands in general; presenting vesicles containing a finely-granular blastema with nuclear particles, imbedded in a fibrous stroma.‡ Two small glands, named respectively the *glandula intercarotica* and the *glandula coccygea* may be enumerated amongst the blood vascular glands. The coccygeal gland§ consists of one or several granules united by connective tissue into a mass about the size of a grain of hempseed, situated close to the ganglion impar. The arteries, derived from the median sacral, possess a very thick, circular, muscular coat, are tortuous, and dilate here and there into small sacculi; the nerves, from the ganglion coccygeum are numerous, and form plexuses with interspersed ganglionic cells. No lymphatics are known to be present. It is believed to be the remains of the vessels which correspond to the lateral branches of the aorta before the tail atrophied in the process of development. The inter-carotid gland resembles the coccygeal, but is of larger size; it contains a very large proportion of medullated nerve-fibres and ganglion cells. The vessels are convoluted and present sacculi; they are derived chiefly from the common carotid, and are believed to be the remains of the third branchial artery (Krause).

The recent researches of Neumann‖ and others seem to demonstrate that

* Poincaré, "Journ. de l'Anat.," 1875, p. 477.

† Kölliker, "Entwickelungsgeschichte," 1879, p. 875.

‡ J. Arnold, Virchow's "Archiv," Band 32, 33, 34; also "Centralblatt," 1864, No. 56.

§ Discovered by Luschka. See Robin's "Journal de l'Anatomie," 1868, p. 269; and Krause, "Histologie," 1876, p. 324.

‖ "Archiv der Heilkunde," 1869, pp. 68 and 220. See also Bizzozero, "Centralblatt für

the so-called "red marrow" occupying the cancellous tissue of the bones constitutes a kind of adenoid tissue in which lymph-corpuscles are developed. The vessels of this tissue are very numerous and large, and are connected by a delicate web of stellate cells, with long processes, the interstices of which are filled by a homogeneous mucin-like material. Imbedded in this are large numbers of cells, presenting every grade of development between lymph and fully-developed white and red blood-corpuscles. These must either gain entrance into the blood vascular system by penetrating the walls of the capillaries, or, as Hoyer thinks, the whole tissue resembles the lacunar system of the lymphatic glands, and the corpuscles are generated by fission of previously existing cells *within* the dilated and anastomosing capillaries. The large many-nucleated cells (myeloplaxes or giant cells) described by Robin as existing in the medulla of bones may possibly, as Neumann surmises, represent the mother-cells of the lymph-corpuscles, or as Bizzozero maintains, such many-nucleated cells with the pigment granules that are often found in them indicate that destruction as well as development of blood-corpuscles takes place in the medullary tissue of the bones. The whole subject has an important bearing on Leucæmia, which is so often associated with disease of osseous tissue. Mosler* observes that marked changes occur in the medulla of bones after extirpation of the spleen.

166. That the Ductless or Vascular Glands, of whose peculiar structure and relations we have thus taken a general survey, have some office of importance to perform in the preparation and maintenance of the blood, cannot any longer be reasonably questioned; and the determination of this point may be fairly regarded as a considerable step in the investigation. It is obvious, from the very copious supply of blood which they receive during the period of their functional vigour, and from the manner in which this is distributed by minute capillary plexuses, on the exterior, and even through the interior, of the glandular vesicles, that it must be subservient to some process of active change; and the aspect of the contents of these vesicles, as well as of the substance in which they are imbedded, indicates that cell-growth is rapidly proceeding, at the expense of the materials thus afforded.

The results of many recent investigations on these organs tend to show that they supply the germs of those cells which are ultimately to become blood-corpuscles. Such, it is well known, was the doctrine of Hewson† in regard to the Spleen and Thymus gland; and there are many facts which lend it a considerable probability. In the first place, we have seen (§ 158, II.) that there is no difficulty in the admission of such corpuscles into the smaller veins of the Spleen; and that there is no physical impossibility in the reception of particles of such a size into the interior of even a closed system of capillaries, is proved by the very curious fact already noticed in regard to the passage of starch-grains into the mesenteric veins (§ 142). Secondly, the spleen undergoes remarkable changes during the period of digestion, and under the influence of the nervous system becoming enlarged in volume with the increased activity of the circulation that takes place in the abdominal viscera soon after the ingestion of food, whilst it contracts when the upper part of the spinal cord and medulla oblongata are stimulated; circumstances suggesting the

die Med. Wissenschaft." 1868, p. 885, and 1869, p. 149; Hoyer, "Centralblatt," 1869, pp. 244 and 257; Palladino, "Centralblatt," 1869, p. 513; and Mosler, "Centralblatt," 1871, p. 290.

* "Centralblatt," 1871, p. 290.

† See his Third Series of "Experimental Inquiries," chaps. iii.–v.

idea that some material is stored up or that some process of growth occurs soon after food is ingested; the substances thus formed entering the vessels when the increased activity of the nervous system consequent on renewed supply of nutrient matter has induced contraction of the splenic musculature. Thirdly, the globular richness of the blood returning from the spleen is absolutely greater than that of the system generally, 1 c. mm. of splenic venous blood containing 5,352,500 red blood-corpuscles, whilst arterial blood generally contains only 5,092,500 corpuscles.* The red corpuscles, moreover, are small, spheroidal, resist the action of water for some time, and do not run into rouleaux, circumstances that favour the view of their recent formation.† Fourthly, if the spleen be extirpated, which has even been performed on man himself, showing that its functions are not indispensable for the preservation of life, the only effects observed have been increase in volume and pigmentation of the lymphatic glands,‡ probably in consequence of their taking on a vicarious action in the development of the white corpuscles. Fifthly, the period of greatest functional activity of these glands generally is during the state of early childhood, when the formative processes are going-on with extraordinary activity; and there is at this time a larger proportion of colourless corpuscles in the blood than at any subsequent period, at least in the healthy state. The relative proportion of the white to the red corpuscles in the splenic arterial and venous blood respectively seems to vary with the previous condition of the organ. Hirt found the proportion of the colourless to the coloured corpuscles to be as 1 : 2000 in the splenic artery, and as 1 : 70 in the splenic vein, but Tarchanoff and Swaen§ observed that the absolute number of white corpuscles is generally greater in arterial splenic than in venous splenic blood, the former containing, in one instance, 8200 white corpuscles in 1 c. mm., whilst the latter contains 7600 white corpuscles in the same bulk. In other instances the disproportion was still greater. A small relative proportion was in their experiments observed when the spleen was caused to enlarge by division of the splanchnic nerves,‖ and such diminution may be attributed either to mechanical arrest and accumulation of the white corpuscles in the spleen or to their destruction in this organ, or, lastly, to their conversion into red corpuscles. Further, as Prof. J. H. Bennett has pointed out, that peculiar condition of the blood, which consists in the multiplication of its colourless corpuscles, is almost always associated with hypertrophy of one or other of these bodies; and in one case of this kind, in which the Thyroid was the organ affected, its cells and their included nuclei were observed to be considerably smaller than usual, and the same peculiarity presented itself in the colourless corpuscles of the blood.¶ Hence there seems a strong probability that whilst the plasma of the blood is being elaborated by these bodies,

* Malassez and Picard, "Comptes Rendus," t. lxxix. p. 1511.

† Hermann, "Human Physiology," translated by Gamgee, 2nd edit. 1878, p. 212.

‡ Fährer and Ludwig, "Archiv f. Phys. Heilk.," 1855, pp. 315 and 491, and others.

§ "Archives de Phys.," 1875, p. 324; and "Comptes Rendus," t. lxxx. p. 125.

‖ Bulgak found the maximum number of white corpuscles in the splenic venous blood when the organ was in its normal condition. These were fewer in the contracted and still fewer in the swollen condition, but if after being swollen the spleen was made to contract by stimulation of the nerves or otherwise, the number of white corpuscles underwent great increase.

¶ This fact is the more weighty, as, in another case observed by Prof. Bennett, the colourless corpuscles of the blood were of two distinct sizes, the smaller corresponding with the nuclei of the larger ones; and the *lymphatic glands* were found to be crowded with corpuscles also of two distinct sizes, exactly corresponding with those of the blood (see "Edin. Monthly Journal," October, 1851).

a constant supply of new blood-corpuscles is also afforded by them;* and that they thus effect for the nutrient materials directly absorbed into the Sanguiferous system that which the glandulæ in connection with the Absorbent system accomplish for the substances which *it* has taken up.†

CHAPTER VII.

OF THE BLOOD; ITS PHYSICAL CHARACTERS, ITS CHEMICAL COMPOSITION, AND ITS VITAL PROPERTIES.

1. *General Considerations:—Quantity of Blood.*

167. From the materials supplied in the Food, there is prepared, by the Digestive and Assimilative processes described in the preceding Chapters, that general nutritive liquid, the *Blood*, which, in the organism of Man (as in that of all the higher Animals) is constantly circulating through its vessels during the whole of life. From this liquid, each portion of the solid tissues has the power of extracting, and of appropriating to its own use, the particular components of its substance; these either pre-existing as such in the blood, or being capable of being readily formed from it by a process of chemical transformation. During its circulation, moreover, the blood draws into its current the effete particles which are set free by the disintegration of the tissues (probably at the very time when it gives-forth the components of the newly-forming structures), and conveys them to the various organs which are provided for their elimination. Hence the Blood not only contains the materials for the renovation of the tissues, but also the products of their decay: but there is an important difference in the proportion of these two sets of components; for whilst the former make-up the principal part of the mass of the fluid, the latter are only detectable in it with difficulty, so long as the excretory organs maintain their normal activity; and only make their presence obvious when they accumulate unduly, in consequence of the retardation or suspension of the eliminating operations.—But besides thus meeting the demand occasioned by the *constructive* operations, and preventing

* This view has been ably supported by Prof. J. H. Bennett, in "Edin. Monthly Journ.," March, 1852; and in his treatise on "Leucocythæmia."

† Some physiologists have arrived at the conclusion, from the modified forms of red blood-corpuscles observed in the splenic-pulp, from their enclosure in amœboid cells, and from the presence of yellowish granules composed entirely of iron oxide (Nasse, indeed, found that the splenic-pulp of old horses contained as much as 5 per cent. of iron, "Sitz-ber. d. Marburg Gesellschaft," 1875, No. 2), that the spleen is a place where the red corpuscles undergo disintegration. The blood corpuscle-holding cells appear to be very active white corpuscles which fasten upon and invest the red corpuscles, and division of the red corpuscles has been observed after they have been thus absorbed (Kusnezoff, "Wiener. Akad. Sitz-bericht,"1873, Band lxxvii., p. 58). The opposite process of the elimination of the fragments of broken-up red corpuscles from the white, has also been observed. (See, for experiments showing the activity of the splenic cells in taking up pigment particles, Ponfick, "Centralblatt. f. d. Med. Wiss.," 1874, p. 384.) A kind of relation appears to exist between the spleen and pancreas, for Schiff found that after ablation of the spleen the pancreatic juice loses its power of digesting albumin, and Herzen observed that whilst the pancreas of a fasting dog digested no albumin, and the pancreas and spleen together of a fasting dog digested no albumin, a mixture of the pancreas of a fasting dog with the spleen of a dog at the seventh hour of digestion, digested albumin freely ("Centralblatt f. d. Med. Wiss." 1877, p. 435).

the results of the *destructive* from exerting an injurious influence on the system, the Blood acts (so to speak) as the carrier of Oxygen introduced from the atmosphere, to the Muscular and Nervous tissues, to whose peculiar vital activity its presence appears to be an essential condition, the same element being also required in various other metamorphoses which form part both of the constructive and of the destructive operations; whilst conversely it imbibes the Carbonic acid, which is one of the chief products of the action of oxygen upon the tissues and fluids of the body, and conveys this to the lungs and skin for elimination.

168. From this variety in the operations to which the Blood is subservient, it naturally follows that the changes which it undergoes in different parts of its circulation are of a very diversified nature, and that the composition of the fluid in the several parts of its course will be far from uniform. Between the blood which is being distributed by the systemic Arteries to the body at large, and that which is being collected from it again by the systemic Veins, after having percolated the tissues, there is not only an obvious difference in hue, which indicates an important change, but there is also a considerable difference in composition, which is revealed by chemical analysis: and a difference of a converse nature presents itself, between the blood that is on its way to be distributed to the Lungs, and that which is returning from them. So again, although there is no obvious dissimilarity in physical characters between the blood which is transmitted to the Liver by the vena portæ, and that which is carried-off from it by the hepatic vein, yet chemical analysis reveals a very remarkable difference in their composition, and shows that the blood of the ascending vena cava (above the entrance of the hepatic vein), that of the right cavities of the heart, and that of the pulmonary artery, differs from all other blood in the body, in constantly containing an appreciable quantity of Glycogen, a peculiar substance readily convertible into sugar, which is formed in its passage through the Liver. In like manner the blood of the renal vein contains a smaller proportion of the chief component of the urinary secretion, urea,* than that of the renal artery; and in many other cases of blood returning from particular organs we know that important differences must exist, although they have not yet been detected by chemical analysis.—In the account to be presently given of the Blood, those most general characters and properties will be first described, which it presents in all parts of its circulation; the principal differences which have been substantiated in the composition of the blood in the several portions of its circuit, will then be noticed; and, lastly, a summary will be given of the most important of those pathological alterations which it exhibits in disease.

169. The quantity of Blood contained in the Human body is probably, for a man of average height, from 12 to 15 lbs.; but its precise determination is more difficult than might at first be supposed. The entire amount which flows from a large arterial trunk freely opened can by no means be taken as a measure; since, however readily it may be permitted to escape, a considerable quantity still remains within the blood-vessels, especially if the heart's action fail before the loss of blood has proceeded very far, so that it is not drawn from the venous system. A closer approximation may be made by opening several vessels at once,† and the proportion of the weight of the blood

* C. Bernard, "Leçons," 1859, vol. ii. p. 31; Picard, "Thèse sur l'Urée," 1856.

† The method adopted by Herbst, "De Sanguinis quantitate, qualis homini adulto et sano convenit." Goettingæ, 1822.

to that of the entire body is then found to be as 1 : 12 in the Ox, as 1 : 16 in the Dog, as 1 : 18 in the Horse, as 1 : 20 in the Goat, Calf, Lamb, and Hare, as 1 : 22 in the Sheep and Cat, and as 1 : 24 in the Rabbit. With these estimates the conclusions drawn by Vanner,* from observations made in the *abbatoirs* of Paris, pretty closely correspond; for he was led by them to the belief that, for horned cattle in general, the proportion does not vary far from 1 : 20. It is obvious, however, that no such method can give more than a *minimum;* since, even after the most complete exsanguination that the freest opening of the vessels can permit, a considerable quantity of blood is still retained in them, and especially in those of the head. Various other methods have been suggested, none of which, however, can be considered as yielding more than approximations to the truth. That of Vierordt† consists in multiplying the quantity of blood which is expelled from the left ventricle at each pulsation of the heart by the number of beats which occur whilst the blood performs one entire circuit of the body. He estimates the former (highly) at 6·3 ozs. av., and the latter at 27·7 beats; consequently the total quantity of blood is about 11 lbs. av., or between one-twelfth and one-thirteenth of the weight of the body. Welcker's method, termed also the "chromatic" or "colour" method, gives nearly the same result for Man and the Dog. It consists in first roughly estimating the quantity of blood in the animal by rapidly bleeding it to death. The portion that still remains in the small vessels is then removed by the injection of distilled water, or of a ·75 per cent. solution of common salt, and the whole body of the animal is finely minced and infused. These liquids are mingled, and on comparing their tint with a series of previously prepared "colour tests," the proportion of blood in which is accurately known, a practised eye may discern variations in the colour when the difference in the quantity of blood does not exceed 4 per cent. It is usual in such cases to administer carbon monoxide to the animal, since this gas, by its action on the red corpuscles, renders the blood of a uniform tint. Welcker estimates that a man weighing 143 lbs. has 11 lbs of blood. An interesting collection of cases has been brought together by Haller‡ of the amount of blood lost by hæmorrhage: and two remarkable instances are cited by Burdach,§ from Wrisberg, who states that a female who died from violent metrorrhagia had lost 26 lbs. of blood, and that 24 lbs. were collected from the body of a plethoric female who had suffered death by decapitation. In the first of these cases, it is probable that, as death could not have been *immediate*, some increase took place from the absorption of the fluids of the body; in the second, however, the suddenness of the discharge of blood, and its concurrence with the destruction of life, must have prevented any considerable augmentation from this source; and if any such increase did take place, it probably did not exceed the amount of blood remaining undischarged in the vessels. An important observation has been made by Bernard,‖ that the quantity of blood which can be obtained from a fasting animal is scarcely more than one-half of that contained in its vessels shortly after a full meal: a point to which no other observer appears to have paid attention, but which may account for some of the discrepancies observable in the different estimates¶. The blood

* "Comptes Rendus," tom. xxviii. p. 649. † "Physiologie," 1864, p. 138.
‡ "Elementa Physiologiæ," vol. ii. pp. 3 and 4.
§ "Traité de Physiologie," traduit par Jourdain, tom. vi. p. 119.
‖ "Leçons," 1859, t. i. p. 419.

¶ Valentin's method is founded on the diminution in the specific gravity of the blood after the injection of a known weight of water into the vessels, and gave for dogs the proportion of the weight of blood to that of body generally as 1 : 4½ ("Repert. f. Anat. und Phys.," Band iii.

is not equally distributed through the several organs and tissues of the body, but is most abundant as a rule in those which perform the most active functions; thus, the largest quantity is found in the liver, of which it forms about 28 per cent. In the spleen and kidney it is present to the amount of about 12 per cent.; in the brain and muscles there are about 5 or 6 parts per cent. by weight; in the bones two and a half per cent., and in the skin about 1 per cent. Worm Müller found that the injection of blood to the extent of 150 per cent. into the vessels of an animal proved fatal usually by rupture of the vessels. After such injection the blood corpuscles undergo regressive changes though more slowly, as estimated by the amount of urea eliminated, than when consumed as food, the process continuing as shown by the increase of urea in the urine for many days.

2. *Physical, Chemical, and Structural Characters of the Blood.*

170. The Blood as it flows-forth from an opening in a large vessel is an apparently homogeneous liquid, possessing a slight degree of viscidity, with a consistence and density somewhat greater than that of water, but especially distinguished by its *colour*, which is usually of a bright scarlet when it is drawn from an artery, and of a dark purple, sometimes almost approaching to black, when it is drawn from a vein. This difference of colour, however, is by no means constant; for arterial blood may sometimes be unusually dark, whilst venous blood is occasionally so florid that it might almost be taken for arterial. The former condition is observable when from any cause the respiratory process is imperfectly effected, as in the fœtus, and it may be especially noticed during operations performed under the influence of anæsthetic agents; it has also been remarked by Dr. John Davy, as usually characterizing the arterial blood of the inhabitants of hot climates,* and it occurs in blood that has been allowed to stagnate either in arteries or veins; but in any of these cases, the ordinary arterial hue is acquired by the blood when it has been sufficiently exposed to the air. The florid hue is presented by the venous blood of animals which are made to respire pure oxygen, and in those poisoned by CO; but it seems normal with some individuals whose respiration is peculiarly active. It is well marked in the blood returning from an actively secreting gland, and from a quiescent muscle.† When ordinary venous blood is examined in thin layers, it presents a deep red or purple tint by reflected light, but by transmitted light it assumes a greenish hue, thus presenting the phenomena of Dichroism; a peculiarity which is not possessed by arterial blood (Brücke): but when the gases of the

p. 281). Blake's method consisted in the injection of a definite quantity of some saline compound, as sulphate of alumina, and its subsequent quantitative determination, in a portion of blood drawn from another part of the system. This means of estimation gives the proportion of blood to that of the body as 1 : 8 or as 1 : 9 (see Prof. Dunglison's "Physiol," 8th edit. vol. i. p. 357), and is in accordance with the results obtained by Lehmann and Weber in their examinations of the quantity of blood discharged from two decapitated criminals (Lehmann, "Lehrbuch," 2nd edit. Band ii. p. 234). (See also Brozeit, Pflüger's "Archiv," 1870, p. 353; Steinberg idem, 1873, p. 101; and Gescheidlen, idem, 1873, p. 350.) Brozeit obtains the Hæmatin by means of ether and hydrochloric acid from a given quantity of the washings after venesection, compares it with that in the same quantity of blood, and makes the requisite calculation. Steinberg proceeds on the principle that solutions of hæmoglobin, when of a certain strength, transmit green light.

* "Anatomical and Physiological Researches," vol. ii. p. 140.—This fact, which harmonizes with the inference to be drawn from the observed results of a high external temperature in reducing the excretion of carbonic acid (CHAP. IX.), is of great practical importance.

† Bernard, "Leçons," 1859, vol. i. p. 324.

blood are wholly removed by exhaustion, both arterial and venous blood assume a deep black colour.* The refractive power of healthy blood on light is from 1·3546, to 1·3494; of serum, 1·3489.†—The *specific gravity* of the Blood is stated by Nasse‡ to vary (within the limits of health) between 1045 and 1075; the average being taken at 1055. The sp. gr. of the Corpuscles is about 1105, and that of the fluid in which they float about 1028. The *chemical reaction* of the blood is invariably alkaline, and very important purposes are served by this alkalinity. The *temperature* of the Blood, usually considered to be about 100° F., has been found to vary several degrees in different parts of the body.§ The blood which has the lowest temperature under ordinary circumstances is that which has circulated through the cutaneous capillaries where it has been exposed to the cooling influences of evaporation and radiation; Bernard, however, ascertained that on carefully enveloping the head or limbs of an animal in cotton wool, the temperature of the arterial and venous blood in the large vessels soon becomes equalized. The blood of the left ventricle again is, for similar reasons, having been transmitted through the pulmonary capillaries, generally‖ of a lower temperature than that of the right. The highest temperature is attained in passing through the glands, muscles, and nerves; for in all such parts, especially during the active performance of their functions, energetic processes of oxidation are being carried on. Hence the blood of the Vena Portæ and other viscera, which has traversed the capillaries of the intestines, spleen, &c., is warmer, especially during digestion, than even the arterial blood; and the blood which possesses the highest temperature in the body, and which is frequently 2° or 3° F. above the ordinary venous blood, is that of the Hepatic Vein, which has been subjected to the active assimilative operation of the liver. The specific heat of the blood of the Ox is on the average 1020.¶—When we add that the Blood has a saltish *taste*, and a faint *odour* resembling that of the pulmonary and cutaneous exhalations of the animal from which it is drawn, we have enumerated all the characteristics which can be made out by the unassisted senses.

171. When the Blood is examined with the Microscope, either immediately upon being drawn, or whilst it is yet circulating in the vessels of the living body (as in the tongue or foot of the Frog, the wing of the Bat, the omentum of the Guinea-Pig,** or any other membranous expansion of similar transparency), it is seen that its apparent homogeneity is not real, but that it consists of two very different components. These are a transparent and perfectly

* Setschenow, "Sitszungsberichte d. Kais. Akad. d. Wiss.," xxxvi. 1859.

† Valentin, Pflüger's "Archiv," 1879, p. 84.

‡ Wagner's "Handwörterbuch der Phys.," Art. 'Blut,' Band i. p. 82.

§ Bernard, "Leçons sur les Liquides de l'Organisme," 1859, iii. iv. v. vi.

‖ See the variable results obtained in Colin's experiments, recorded in the "Ann. d. Sci Nat.," Ser. v. t. vii. 1867, p. 83. Jacobson and Bernhardt found the temperature of the Left Heart to be from 0°·12 to 0°·42 Cent. warmer than the Right, as ascertained by the introduction of a compound needle connected with a thermometric apparatus through the parietes of the chest into the cavity of the ventricles (see "Centralblatt," 1868, p. 689). Körner, however ("Inaug. Dissert.," Breslau, 1871), and Heidenhain (Pflüger's "Archiv," Band iv. 558) support Bernhardt's statements. Albert and Stricker (Stricker's "Jahrbücher," 1873, p. 29) found a thermometer inserted into the *substance* of the muscular tissue of the left ventricle, stood 0°·5–0°·7 Cent. higher than when introduced into the *cavity* of the same ventricle in the living animal, which may in part explain the discrepancy in the different experiments. John Davy thought the blood in the left ventricle to be about 1° F. warmer than that of the right; but unless special precautions were taken to prevent loss of heat through the thin walls of the right ventricle, this is only what might be expected ("Researches Physiol. and Anatom.," 1839, vol. i. p. 149).

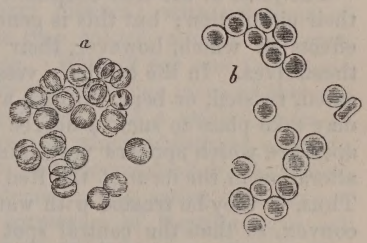
¶ Gamgee, "Journ. of Anat. and Physiol.," vol. ii. p. 139.

** See Burdon Sanderson, "Handbook for the Physiological Laboratory," 1873, p. 231.

colourless liquid which is known as the Plasma or *Liquor Sanguinis*, and a set of *Corpuscles* which are suspended in it:* these, when seen in mass, present a distinctly *red* hue, and it is to their presence alone that the colour of the blood is due; but there are also to be seen, scattered among the red, a few which are *colourless*, and which differ from the red in some other particulars presently to be noticed. If the recent observations of Dr. Norris, of Birmingham,† be substantiated, there are in addition a large number of transparent colourless cells, the presence of which can only be demonstrated by special methods of research. 100 vols. of human blood contain about 64 vols. of plasma, and 36 vols. of corpuscles.‡

172. The *Red Corpuscles* of the Blood (commonly, but erroneously, termed "globules") are minute, nearly transparent bodies of a flattened or discoidal form, which, in Man, as in most of the Mammalia, have a well-defined circular outline (Fig. 103, *b*). When isolated they appear of a yellowish-green tint, the red colour being only presented when there are several layers. The surfaces are somewhat concave; and there is a bright spot in the centre, which has been regarded by many as indicating the existence of a nucleus; though it is really nothing else than an effect of refraction, and may be exchanged for a dark one by slightly altering the focus of the Microscope (Fig. 103, *a* and *b*). The margin is sometimes crenulated. The *number* of the red corpuscles is about 4·5 millions in 1 c. mm. (or $\frac{1}{25}$th inch square) in women, and about 5 millions in men, with about 14,000 colourless corpuscles; upon which estimate there are about 250 thousand millions of red corpuscles in 10 lbs. of blood. The number of red corpuscles is greater in winter than in summer, in the country than in the town; under all circumstances causing diminution of the fluid part of the blood, as after the action of carthartics, and after moderate fasting. It is observed also to increase soon after eating, probably owing to a demand upon the fluid of the blood by the secreting organs. The globular richness is very high during the first day after birth, but it progressively diminishes in the course of the next ten days, since at this time there is a rapid growth of the child, with increase in the proportion of serum. The globular richness of the blood diminishes after long fasting, and the consumption of a large quantity of fluid, after want of sleep, and after sharp exercise.§ Vierordt observed a reduction in Marmots after long hybernation, from 7 millions to 2 millions in 1 c. mm. The number of corpuscles varies in different parts of the circulation, the largest number being contained in the small cutaneous veins, and a smaller proportion in the larger arteries and veins. It also varies with age.‖ Thus, from $2\frac{1}{2}$ to 15 years the red corpuscles vary from 2160000 to 5502000, the mean being 4269911. From 20 to 30 years they vary from 3399395 to 4899375, the mean being 4192687; and

Fig. 103.



Red Corpuscles of *Human Blood:* represented at *a*, as they are seen when rather beyond the focus of the microscope; and at *b*, as they appear when within the focus.

* First seen by Swammerdam in the Frog in 1658, and by Leeuwenhoek in Man in 1673.

† Paper read at Cork Meeting of Brit. Med. Assoc., 1879.

‡ Klein and Noble, "Atlas of Histology," p. 1, 1879.

§ See G. Thin, "Lancet," 1878, vol. i. p. 126; Malassez, "De la numération des globules rouges du Sang."

‖ See Dubrisay, "Gaz. Med.," 1878, No. 15.

from 30 to 55 years they vary from 3266250 to 5904375, the mean being 4080113. The mean of all Dubrisay's numerous observations was 4177109. Amongst animals the blood of the Carnivora contains more red corpuscles than that of the Herbivora. Malassez found 3·5 millions in 1 c. mm. in the rabbit; 18 millions in the goat; 10 millions in the camel; 2 to 3·3 millions in the cock; 700,000 to 2 millions in osseous fishes; 140,000 to 230,000 in cartilaginous fishes.* The richness of the blood is not, however, dependent alone on the number of the corpuscles, but upon their volume and the quantity of hæmoglobin they contain. The Corpuscles of Man and Mammalia seem to be homogeneous masses of germinal matter, soft, elastic, transparent, and structureless, refracting light singly, and having a specific gravity of about 1·105. The appearances of a proper cell-wall and nucleus which they present when subjected to the action of certain reagents† are probably deceptive, and arise either from physical or chemical changes occurring on their surface or in their substance. The average diameter of the red corpuscles is about 1-3200th of an inch (Gulliver), or 0·0077 mm. (Welcker), some, however, being as much as one-third larger and others one-third smaller than the average.‡ The thickness is about 1-12400th of an inch, or 0·0019 mm.§ The volume of each is estimated at 0·000000077217 of a cub. millimetre, the superficies at 0·000128 of a square mm., and the superficies presented by all the corpuscles together a square of 80 military steps to the side. The weight of a single corpuscle is estimated at 0·00008 mgrm.

The *form* of the Red Corpuscles is not unfrequently seen to change during their circulation; but this is generally in consequence of pressure, from the effects of which, however, their resiliency enables them to quickly recover themselves. In the capillary vessels they sometimes become suddenly elongated, twisted, or bent, through a narrowing of the channel; and this change may take place to such a degree as to enable the disc to pass through an aperture which appears very minute in proportion to its diameter. Great alteration in the form of the Red Corpuscles is effected by various reagents. Thus, if they be treated with water, they first become flat, and then double-convex, so that the central spot disappears; and by a continuance of the same process, they at last become globular, and so attenuated that a diffusion of their substance seems to take place through the surrounding liquid.‖

* In Malassez's method of numbering the corpuscles, the blood is drawn into a capillary glass tube of known capacity, diluted with a definite quantity of serum, and the corpuscles counted. See also Gower's 'Hæmatocytometer,' "Lancet," vol. ii. 1877, p. 799, and 1878, vol. ii. p. 901. (Cutler and Bradford, "Journal of Physiology," vol. i. p. 427, 1878–79, which last contains many references.)

† Dr. J. G. Richardson, of Philadelphia ("On the Cellular Structure of the Red Blood Corpuscle," Pamphlet, 1870), adduces arguments to show that the red corpuscles of the *Menobranchus*, or *Proteus* (*Batrachia*), are truly cellular. On division the contents escaped, and the cell-wall collapsed, and crystals were frequently found in the interior, over which the cell-wall appeared to be stretched like a tent over a tent-pole. Prof. Böttcher believes he has obtained evidence of the presence of a nucleus by treating blood with an alcoholic solution of corrosive sublimate ("Quart. Journ. of Mic. Sci.," 1877, p. 377. See also Hammond, "Month. Journ of Mic. Sci.," 1877, p. 147).

‡ Hayem, "Centralblatt," 1879, p. 366, describes small peculiar corpuscles, which he names "Hæmatoblasts," and believes to serve for the renovation of the red corpuscles.

§ The diameter of the corpuscles bears no constant relation to the size of the animal, even within the limits of the same Class; thus, although those of the Elephant (2, Fig. 105) are the largest among Mammalia (as far as is hitherto known), those of the Mouse tribe are far from being the smallest, being, in fact, more than three times the diameter of those of the Musk Deer (3, Fig. 105). There is, however, as Mr. Gulliver has remarked, a more uniform relation between the size of the animal and that of its blood-discs, when the comparison is made within the limits of the same Order.

‖ A large number of experiments of this kind were made, and their results accurately

With dilute solutions of common salt they become prickly on the surface, so as to resemble the fruit of the horse-chestnut (Fig. 104, *c*). The pro-

Fig. 104.

Various forms assumed by blood corpuscles after withdrawal from the body. The first represents an oval corpuscle of the frog breaking up into segments. The corpuscle marked *a* exhibits the formation of a crystal within a red corpuscle (Owsjannikow). *b*, *c*, *d*, forms represented by Böttcher. The remainder are from Mr. Gulliver's drawing.

jections, seen in profile, give the corpuscles a stellate form, and those seen *en face* appear as black dots. With acetic acid the corpuscles become globular and pale, but their outlines remain distinct; with solutions of magenta they swell up and assume a faint rose colour, a dark red spot appearing on some point of their circumference. With (2 per cent.) solutions of tannin,* after the lapse of twenty or thirty seconds some point of the circumference of the red corpuscle appears to give way and a small button of highly-refractile yellowish-green substance projects which sometimes contains a vesicular body that may again be retracted into the corpuscle by the action of acetic acid. The similar appearances produced by the action of a one per cent. solution of Boracic Acid on the red corpuscles of Reptilia have led Brücke† to regard the Blood corpuscles in these animals as consisting of a transparent shell or case, the '*œcoid*,' which is occupied by the '*zooid*,' the latter being composed of the nucleus and the hæmoglobin. If carbonic acid gas be transmitted through a drop of blood which has been mingled with a little saline solution so that the corpuscles have become horse-chestnut-shaped, the stellæ disappear, and although there are many which do not reassume their natural biconcave form, remaining saucer-shaped, yet their surfaces become smooth and even. On the transmission of air they again become horse-chestnut-shaped, and this alternating effect may be repeated several times. Klein‡ suggests that the action of tannin and boracic acid is due to phenomena of coagulation, and that of carbonic acid gas to the re-solution of a spontaneously coagulated constituent. Bile and Urea, according to Kühne, dissolve the red blood cells, though Jurasz§ maintains that they only swell up and burst; the addition of Urine seems to exert no other influence upon them

recorded, by Hewson (see his "Inquiry into the Properties of the Blood," 1782, and his "Description of the Red Particles of the Blood," 1788). See also the Lectures by Mr. Gulliver, delivered at the College of Surgeons in 1862–63, in *Med. Times and Gazette*.

* Roberts, "Proceed. of Roy. Soc.," vol. xii. 1863, p. 481. See Addison, "Proceed. Roy. Soc.," Dec. 8, 1859; and Pouchet, "Traité d'Histologie," p. 219.

† See his "Vorlesungen über Physiolog.," 1874, p. 73.

‡ "Handbook to the Physiol. Laboratory," p. 16.

§ "Inaug. Diss. Greifswald."

than a saline solution of equal density would do, as was long since ascertained by Hewson. Alkalies cause the corpuscles to swell and to become cup-shaped, after which they lose their colour and disappear. The passage of a current of electricity produced by the discharge of a Leyden jar (having a surface of 500 square centimetres) at intervals of from three to five minutes, causes the circular discs to become slightly crenate, then rosette-shaped and horse-chestnut-shaped; still later the processes are withdrawn and the corpuscles become round and pale, giving up their colouring matter to the surrounding fluid.* If blood be exposed to a temperature of 140° or 150° F., or if it be frozen and then thawed once or twice, or if the whole of the gases be removed by the air-pump, the corpuscles disappear, the colouring matter stains the serum of a lake colour, and only a few flocculi remain.† Professor Lehmann has remarked‡ that some of the red corpuscles resist the influence of reagents much more than others do, and he infers that the latter are the older cells as having the strongest tendency to disintegration. It is probable that the Blood-corpuscles, even whilst they are circulating in the living vessels, are liable to alterations of form from variations in the density of the fluid in which they float; and that such alterations may be constantly connected with certain disordered states of the system.§ Thus, even without such an alteration in the Blood as would constitute disease, its proportion of water may be temporarily so much diminished by diuresis or excessive perspiration, unbalanced by a corresponding ingestion of liquid, that the corpuscles may be made to present a granulated edge; which is rendered smooth again by the dilution of the liquor sanguinis with water. We hence see the necessity, in examining the Blood microscopically, of employing a fluid for its dilution that possesses as nearly as possible the same characters as the ordinary 'liquor sanguinis.' In the accompanying Fig. (105), which shows the form and size of the red blood-corpuscles of animals belonging to each division of the Vertebrate class, most accurately drawn to scale by Mr. Gulliver,‖ it will be seen that whilst in Man and all Mammalia they are destitute of a nucleus, or *apyrenæmatous*,¶ and with the exception of the Camel tribe circular (4), in Birds, Reptiles, and Fish, except only some of the lowest forms of the last, the corpuscles are uniformly oval and nucleated, or *pyrenæmatous;* in the Camel tribe, though the corpuscles are oval, yet they conform to the Mammalian type in being free from a nucleus, and in their small size. Mr. Gulliver has particularly insisted on this difference between the blood of the Mammalian and Oviparous Vertebrata, maintaining it to be the only single, universal, and characteristic difference between them.** In embryonic life, however, the red corpuscles even of Mammals possess a nucleus.

173. The Red Corpuscles, when freely floating in the liquor sanguinis of blood no longer in motion, exhibit a marked tendency to approximate one another; usually coming into contact by their flattened surfaces, so that a number of them thus aggregated presents the appearance of a pile of coins; or, if the stratum be too thin to permit them to lie in this manner, they partially overlap, or even adhere by their edges, which then frequently become polygonal instead of circular. The corpuscles when thus adherent, resist the

* Klein, op. cit. p. 17. See also Böttcher, Virchow's "Archiv," Band xxxix. 1867, p. 427.

† Rollett, "Versuchen über das Blut. Wien Sitz-ber. M. Nat. Wiss." Abt. ii. Band xlvi. p. 65.

‡ Op. cit. vol. ii. p. 184.

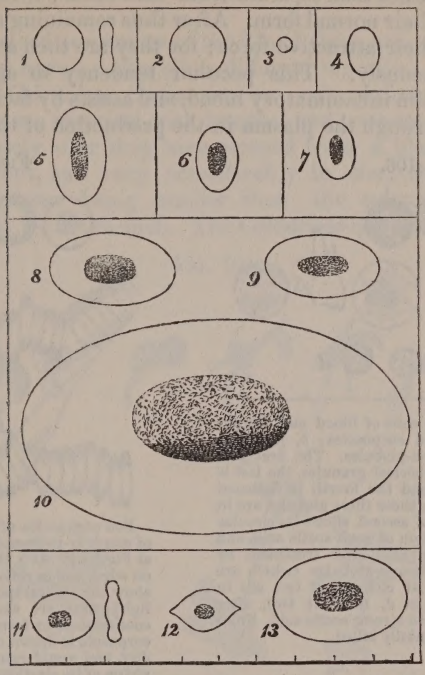
§ See Dr. G. O. Rees' 'Gulstonian Lectures' in the "Medical Gazette" for 1845.

‖ See "Proceedings of the Zoolog. Soc. of London," 1862, p. 101.

¶ *a*, not, *πυρὴν*, a nucleus, and *αἷμα*, blood.

** The following measurements of the blood of domestic animals (expressed in vulgar

Fig. 105.



All the Corpuscles here shown are drawn to the uniform scale, at the bottom of the wood-cut, of 1-4000th of an English inch, and the measurements are expressed in vulgar fractions of that inch. T. D. signifies transverse diameter; L. D. long diameter; S. D. short diameter.

	T. D.	L. D.	S. D.
MAMMALIA.			
1. Red Corpuscle of Man, seen on the flat surface and also on the edge; thickness 1-12,400	1-3200		
2. „ „ of Elephant	1-2745		
3. „ „ of Musk Deer	1-12325		
4. „ „ of Dromedary, thickness 1-15,337		1-3254	1-5921
AVES.			
5. „ „ of Ostrich		1-1649	1-3000
Nucleus of ditto		1-3200	1-9163
6. „ „ of Pigeon		1-2314	1-3429
7. „ „ of Humming Bird		1-2666	1-4000
REPTILIA.			
8. „ „ of Crocodile		1-1231	1-2286
9. „ „ of Python		1-1440	1-2400
10. „ „ of Proteus		1-400	1-727
PISCES.			
11. „ „ of Perch		1-2461	1-3000
12. „ „ of Pike		1-2000	1-3555
13. „ „ of Shark		2-1143	1-1684

fractions of an English inch) have been selected from Mr. Gulliver's observations, as the most likely to become of interest in Juridical inquiries:—

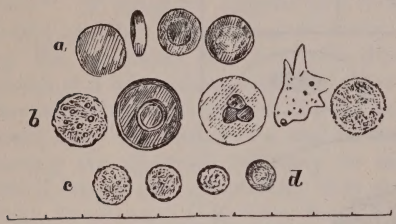
Man 1-3200	Mouse 1-4230	Cat 1-4404
Dog 1-3532	Ass 1-4267	Horse 1-4600
Hare 1-3560	Pig 1-4230	Sheep 1-5300
Rabbit 1-3607	Ox 1-4267	Goat 1-6366
Rat 1-3754	Red Deer . . . 1-4324	

For a critique showing that too much reliance must not be placed upon them, see Woodward, "Month. Mic. Journ.," Feb. 1, 1875.

A Tabular summary of Mr. Gulliver's very numerous and accurate measurements of the

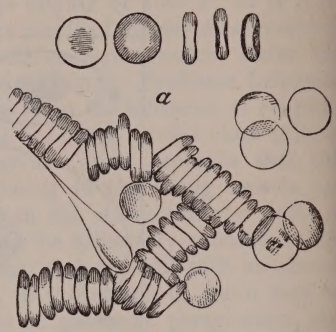
influence of forces which tend to detach them, and will even undergo considerable change of shape, rather than separate from each other; if forced asunder, however, they resume their normal form. After thus remaining adherent for a time, they seem to lose their attractive force; for they are then seen to separate from each other spontaneously. This peculiar tendency to aggregation is most strongly manifested in inflammatory blood, and assists by facilitating the descent of the corpuscles through the plasma in the production of the buffy coat. It has

Fig. 106.



Red corpuscles and pale cells of blood and lymph-globules. At *a*, four red corpuscles; *b*, five pale globules; *c*, *d*, four lymph-globules. The first pale globule at *b*, contains spherical granules, the last is only minutely granular, and the fourth is flattened and sending off processes: these three globules are in the natural state, but the second shows its circular nucleus exposed by the action of weak acetic acid, and the third the nucleus divided after treatment by stronger acid. Of the lymph-globules (which are from an inguinal gland) at *c*, the first two are in their natural state; and at *d*, the last two, after having been long steeped in strong acetic acid. From a child, aged three, accidentally killed.

Fig. 107.



Red corpuscles of *Man* (on the same scale of one-four-thousandth of an inch, as marked at Fig.105). At *a*, the corpuscles are seen flat on edge, and in rolls; the two first corpuscles show the central spot or concavity, dark and light: next are shown the biconcave and concavo-convex forms; among the rolls, one corpuscle is drawn out by virtue of its viscidity, and would resume its circular shape by virtue of its elasticity.

been regarded by some* as a purely physical phenomenon, on the ground that it can be imitated to a certain extent by partially immersing poised cork discs in water or other liquid, when the particles of the solid outside the liquid are found to have an attraction for each other, leading to movement through very sensible distances. But in the blood we have to deal with wholly submerged discs, and it is probable that a more correct explanation is that the corpuscles are rendered adhesive by the formation of fibrin between them, since if the chains be forcibly broken up, the separated corpuscles may often be seen to be still connected by fine threads, whilst various circumstances, such as the addition of salt, tending to promote, retard, or prevent the formation of fibrin, tend also to accelerate or prevent the appearance of rouleaux.† The proportion of the red corpuscles to the plasma or liquid in which they float is, in the horse, in 1000 parts, as 344·18 : 655·82, and in the pig as 436·8 : 563·2.‡ 1000 parts by weight of the moist red corpuscles of the dog contain water 569·3,

Red Corpuscles of the Blood of different animals, from all the classes and most of the orders of the Vertebrate series, is contained in the "Proceedings of the Zoological Society," No. cii., and also in his edition of the "Works of Hewson," already referred to, published by the Sydenham Society (p. 237). Manassein ("Centralblatt," 1871, p. 689) finds that agents or conditions which lower the temperature of the body, as Muriate of Quinine, Alcohol and Acute Anæmia, effect enlargement of the blood-corpuscles, whilst they are diminished in size by agents exalting the temperature of the body, as Heat, Septicæmic poisoning, and exposure to Carbonic Acid. They enlarge under exposure to Oxygen. Lastly, in certain diseases, as in pernicious Anæmia, they vary in size, many being far below the normal diameter.

* Dr. Norris, "Proceed. of Roy. Soc.," No. 112, 1869.

† See J. Dogiel, "Archiv f. Anat. v. Physiologie," 1879, p. 222. For another explanation see Lister, "Phil. Trans.," 1858.

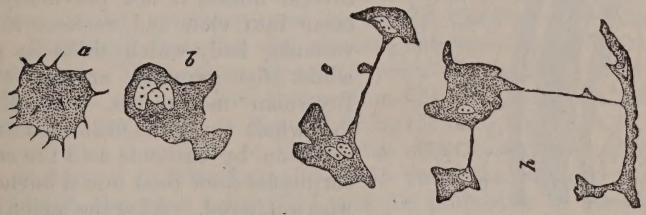
‡ Hoppe-Seyler, "Phys. Chemie," 1879, p. 447.

solids 430·70. Of the 430·70 parts of solids, hæmoglobin and albumin constitute 412·51 parts, cholesterin 1·26, lecithin 7·47, extractives 2·97, inorganic salts 6·49.*

174. Besides the red corpuscles of the blood there are others which possess no colour and may have an altogether different function. These are known as the *White or Colourless Corpuscles*, or not unfrequently Leucocytes (Fig. 108). They are identical with lymph- and pus-corpuscles, and when examined immediately after they have escaped from a blood-vessel are spherical and transparent, and vary considerably in size, the greater number being larger, but some being smaller than the coloured corpuscles, the average being about 1-2500th inch. The Colourless corpuscles possess a higher

Fig. 108.

Fig. 109.



Various forms assumed by the white corpuscles of the blood. The upper row represents the white corpuscles of Man; the lower row, white corpuscles from the Newt, showing changes effected in 15 minutes.

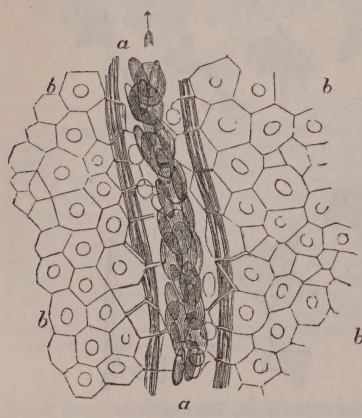
refractive power than the red; from which they are further distinguished by their greater firmness, their inferior elasticity, and lower specific gravity, their softly shaded and granular aspect, and the absence of any disposition to adhere to each other; so that, when a drop of fresh blood is placed between two strips of glass, and these are gently moved over one another, the white corpuscles may be at once recognised by their solitariness, in the midst of the rows and irregular masses formed by the aggregation of the red. This is still better seen in inflammatory blood, in which the Red Corpuscles have a peculiar tendency to adhere to one another, so that the distinctness of the White is more marked. They also differ from the red in their power of ingesting foreign particles and in their ubiquity, being formed in all the tissues both within and outside of the blood-vessels, and they have hence been termed migrating or wandering cells. They appear to be composed of protoplasm, and are destitute of an investing membrane. Under favourable circumstances, as when examined on a warm stage, they exhibit well-marked amœboid movements.† The mass of protoplasm of which each is formed presents a network of very fine contractile fibrils termed the "intra-cellular network," in the meshes of which a hyaline interstitial substance is contained. One or two nuclei, not always visible in the fresh and living condition, come into view

* Hoppe-Seyler and Hohlbeck, Hoppe-Seyler's "Physiol. Chemie," 1879, p. 402.

† Garrod suggests (*Times*, Jan. 23, 1878) that the amœboid movement may be growth in the direction of nutriment. See Preyer, Virchow's "Archiv," 1864, p. 417.

after removal from the body, which contain a similar network, termed the "intra-nuclear network," the fibres of which are in direct connection with those of the intra-cellular network.* Some of the characteristic changes of form are shown in Figs. 108 and 109. Colourless corpuscles may be readily distinguished in the blood circulating through the small vessels of the Frog's foot; and it is then observable that they occupy the quiescent layer, or exterior of the current, where the motion of the fluid is slow, whilst the *red* corpuscles move rapidly through the centre of the tube (Fig. 110). The colourless corpuscles, indeed, often show a disposition to adhere to the walls of the vessels; which is manifestly increased on the application of an irritant. In inflammatory states, or even when the circulation is merely checked in any part, the white corpuscles have a great tendency to escape through the vessels into the adjoining tissues or cavities of the body, and the term *diapedesis* is applied to the process by which they traverse the vascular walls. On the addition of distilled water the white corpuscles swell up, become globular, and cease to move; one or several nuclei, if not previously visible, come into view and coalesce to form a vesicular body which shifts its position, whilst the granules around it exhibit Brownian movements, and ultimately the whole corpuscle disintegrates. When acted on by carbonic acid the colourless corpuscles show their nuclei but are otherwise unaltered. After the action of acetic acid they present the appearance of globular bodies in which two, three, or more small shrunken nuclei are visible. In alkalies the colourless corpuscles swell and rapidly disappear, yet they exhibit remarkable resistance to the action of bile.† When excited electrically during their amœboid movements they assume the spheroidal form, but resume their activity on the cessation of the stimulus; after repeated excitation they expand and flatten, but still exhibit changes of form. Under the influence of successive shocks of greater intensity they swell, the granules exhibit molecular movements, and they finally disappear.‡ Quinine has a remarkable power of arresting the movements of the white corpuscles.§ The stroma of the white corpuscles contains a substance analogous to Myosin, with Lecithin, Cholesterin, Glycogen, and Fat. In addition to the alkaline albuminates and serum-albumin, the nucleus contains nuclein and lecithin.‖ Hoppe-Seyler finds

FIG. 110.



A small Venous trunk, *a*, from the Web of the *Frog's* foot; *b*, *b*, cells of pavement-epithelium, containing nuclei. In the space between the current of oval Blood-corpuscles, and the walls of the vessel, the round transparent colourless corpuscles are seen.

* See Klein and Noble, "Atlas of Histology," 1879, p. 5.

† Jurasz, "Inaug. Diss. Greifswalde," 1871.

‡ Klein, op. cit. p. 18. See also Golubew, "Wien. Akad. Sitz.," lvii. p. 555, Math. Nat. Classe.

§ Binz, *Practitioner*, No. 51, 1872.

‖ See Hoppe-Seyler and Miescher in Hoppe-Seyler's "Med.-Chem. Untersuch.," Band iv. 1872, pp. 441 and 502, quoted in Brunton and Ferrier's 'Report on Physiology' in "Journ. of Anat. and Phys.," vol. vi. p. 450. Also Brunton's paper on the Chemical Comp. of the Nuclei of Blood Corpuscles in "Journ. of Anat. and Phys.," vol. iv. 1870, p. 91. The distinctive chemical characters of 'nuclein' appear to constitute an answer to Mr. Savory's view that "the existence of a nucleus in the red corpuscles of Ovipara is due to changes after death or removal from the vessels. See his paper in "Month. Micr. Journ." 1869, vol. i. p. 235.

that the white corpuscles only contain glycogen as long as they exhibit movements, and that when they become rigid they lose their glycogen and contain sugar. The white corpuscles of the blood, both of the frog and triton, as well as those of man, have been observed by Klein to multiply by fission ;* but they are essentially regenerated from lymph corpuscles of lymphatic glands and from certain endothelial cells of the serous membranes.

The proportion which the white or colourless corpuscles bear to the red, is very small in the blood of man and the higher Vertebrata ; being, in the state of health, according to the estimate of Moleschott (which is confirmed by Kölliker),† not more than 2·55 to 1000. Some discrepancy exists in the statements made by competent observers in regard to the influence of food. Thus, according to Hirt, of Zittau,‡ in the morning before breakfast the proportion is one colourless to 716 coloured corpuscles ; half an hour after breakfast 1 : 347 ; between two and three hours after breakfast 1 : 1514 ; ten minutes after dinner 1 : 1592 ; half an hour after dinner 1 : 429 ; two hours and a half to four hours after dinner 1 : 1481; half an hour after supper 1 : 544 ; and between two and a half to three and a half hours after supper 1 : 1227. Cutler and Bradford,§ however, observed an increase in the globular richness of the white corpuscles during a fast, and a decrease after a meal. The white corpuscles are more abundant in children than in adults, and there is an increase during pregnancy and in certain diseased conditions of the system. Dubrisay‖ finds that the absolute number of the white corpuscles varies with age. Thus, from 2½ to 15 years the number of white corpuscles in 1 cub. mm. of blood varies from 761 to 12,181, the mean being 6704, and the proportion to the red being 1 : 648; from 20 to 30 years the number varies from 2284 to 11,306, the mean being 6113, and the proportion to the red 1 : 700; from 30 to 55 years the number varies from 2512 to 14,465, the mean being 6931, and the proportion to the red 1 : 616. The mean of all observations, which were very numerous, gave 6307 white corpuscles in 1 cub. mm. of blood, and the proportion to the red 1 : 683. In the oviparous Vertebrata the proportion is higher ; thus, it has been observed by Wagner¶ to be as 1 : 16 in the blood of a frog examined in February, and as 1 : 6 in similar blood examined in August. In one vertebrated animal, the *Amphioxus*, the red corpuscles are wanting altogether ; their place in the circulating blood being taken by the colourless. And in the invertebrate series generally, the corpuscles of the circulating fluid correspond rather to the *colourless* corpuscles of the blood of Vertebrata, and to the corpuscles of lymph and chyle (which may be regarded as the same bodies in an earlier stage of development), than they do to the *red* corpuscles, which are peculiar to Vertebrata.** Thus, in one of its most characteristic features, the blood of Invertebrata†† (and of Amphioxus) may be likened rather to the lymph and chyle of vertebrated animals than to their blood ; and this resemblance is strengthened by the fact that there is no distinction in the former between the

* "Centralblatt," 1870, p. 17.

† "Manual of Human Histology" (Sydenham Society's edition), vol. ii. p. 330.

‡ Müller's "Archiv," 1856, p. 174 ; see also the Experiments of Marfels and Lorange, quoted in Ludwig, vol. ii. p. 38, 1861.

§ Foster's "Journal of Physiology," vol. i. 1878–79, p. 433.

‖ "Gaz. Med.," 1878, No. 15, and "Centralblatt," 1878, p. 703.

¶ "Elements of Physiology," translated by Dr. Willis, p. 246.

** See Mr. Wharton Jones's Memoir on 'The Blood-Corpuscle considered in its Different Phases of Development in the Animal Series,' in the "Philos. Trans.," 1846 ; also "Princ. of Comp. Phys.," 4th edit. §§ 379–382.

†† Except in a few cases, such as Solen, Siliqua, Sipunculus, and in the common earthworm, in which the corpuscles appear to be truly respiratory in function.

absorbent and the *sanguiferous* vessels, which in the latter respectively contain the nutritious fluid in its earlier and in its later stages of development. Moreover, the earliest blood-corpuscles of the embryo of even the highest Vertebrata are colourless; and long after the blood has acquired its characteristic hue from the development of red corpuscles, the colourless corpuscles bear a very large proportion to the red, so as even to equal them in number (as the author is informed by Mr. Gulliver), in the blood of fœtal deer an inch and a half long, and absolutely to preponderate in the blood of still smaller embryos.

175. Dr. Norris, examining the blood in extremely thin layers* observed that the red corpuscles as they moved in the plasma often presented indented outlines, apparently in consequence of these impinging against some unseen circular bodies. Further research has led him to conclude that the blood contains a large number of transparent corpuscles of the size of the red discs, which, under ordinary circumstances, are invisible, because their refractive index and colour coincide with those of the plasma. The outlines of these transparent corpuscles are best brought into view by altering the refractive index of the plasma, as by pricking the finger through a minute drop of a saturated solution of common salt and permitting the fluid to run between the closely approximated surfaces of the glass. Dr. Norris finds that by taking advantage of the tendency of these corpuscles to adhere to solids, they may be withdrawn from the plasma, and if at the moment of isolation the adherent groups are exposed to the vapour of osmic acid, especially at a temp. of 0° C., the form of the corpuscles is preserved and they are found to be colourless biconcave dics. The corpuscles may be stained whilst still contained in the plasma by the addition of a strong solution of carmine in an ammoniated and saturated solution of common salt. They then first appear as delicate white discs, floating in the coloured fluid and contrasting strongly with the red discs, but soon disappear by assuming the same tint as the stained plasma; finally, they reappear, having acquired a deeper tint than the surrounding fluid. In investigating the *source* of these colourless transparent biconcave discs, between which and the red discs corpuscles of every gradation of colour may be seen, Dr. Norris observed that the morphological elements of the spleen and lymphatic glands are liable to considerable changes, both of size and form, and that when examined with due precaution the lymph-corpuscles appear as discs of the same diameter as the red corpuscles, with depressions on the surface, giving them a granular aspect, and representing, as he believes, the commencement of the process by which the disc is rendered biconcave. They then enter the blood and become invisible, in consequence of their having the same colour and refractive index as the blood plasma, remaining in this state till they have acquired sufficient colour to contrast slightly with this liquid, when they reappear as pale ordinary red corpuscles, before which period their biconcave form is perfected.

176. If the blood of a Mammal be exposed drop by drop to a cold of 8° or 9° Fahr., and then be rapidly warmed to 68° Fahr., the corpuscles will be found to have lost their colour, whilst the serum is deeply stained. A kind of analysis of the constituents of the blood may thus be effected. To the material of the corpuscles, which retain for some time their original form and elasticity, though devoid of colour, the term *Stroma* has been applied,

* The blood was allowed to occupy the space between a flat slide and a slightly convex cover glass strapped firmly down upon the slide, so as to exhibit Newton's rings, the two glasses being less, therefore, than 1–10,000th of an inch apart, and the corpuscles being examined on the flat surface and in single layer. (Demonstration given by Dr. Norris at Cork Meeting, Brit. Med. Assoc. 1879.)

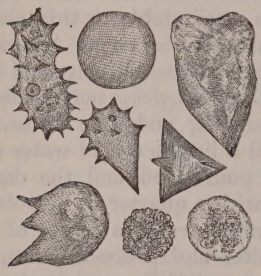
whilst the colouring matter has been named *Oxyhæmoglobin*, Hæmatoglobulin, or Hæmatocrystallin, and is characterized by its property of assuming under favourable circumstances the crystalline form. The *stroma* appears from its reactions to be chiefly composed of *albuminous compounds*, the nature of which has not been clearly ascertained, together with *lecithin*, *cholesterin*, and salts. The colouring matter of the blood, which forms 12 to 15 per cent. of the total mass of the blood, or from 86 to 94 per cent. of the organic constituents of the red corpuscles, appears to exist in two states, Hæmoglobin and Oxyhæmoglobin. Both are contained in venous blood, but only the latter in arterial, the affinity of Hæmoglobin for oxygen being so great, that in traversing the capillaries of the Lungs, where it is brought into relation with air, it absorbs oxygen, and is immediately converted into Oxyhæmoglobin, becoming at the same time much brighter in colour. On the other hand, in traversing the systemic capillaries a portion of the Oxyhæmoglobin loses its oxygen and becomes converted into Hæmoglobin, which is of a darker hue. The difference in colour between arterial and venous blood is in great measure attributable to this chemical change. Hoppe-Seyler has suggested the use of the terms Arterin and Phlebin for the oxidised and reduced Hæmoglobin respectively, and Stokes has named them scarlet and purple Cruorin. *Oxyhæmoglobin* may be obtained by mixing freshly-drawn blood with common salt, and thus allowing the corpuscles to sink. The plasma is decanted, and a little ice-cold water added. The mass is agitated with cold ether, which is poured off, and the dark-red watery solution is filtered quickly, mixed with a quarter of its volume of cold alcohol, and allowed to stand for several hours at a temp. of about 20° F. The crystalline mass is placed on a filter and pressed, then quickly dissolved in a little water at 70° F.; on cooling to 32° F. precipitation with ice-cold alcohol, and putting aside at temp. below 32°, crystallization can be effected.* Oxyhæmoglobin is very unstable; it undergoes decomposition even in being desiccated, and a fibrin-like body, a substance resembling serum-albumin, and a colouring matter are produced, which last resembles Hæmatin in acid solution in its spectrum, whilst it differs from it in being soluble in water and in dilute acids. All acids act upon solution of Oxyhæmoglobin, even at a temperature of 40° F. The bright-red solution becomes dark-red or brown, and it no longer presents dichroism. In this decomposition albumin is separated, which if it remain in solution is Syntonin, and a new colouring matter is formed, which, according to the nature and strength of the acid, may either contain albumin, and is then named Methæmoglobin, or be free from albumin, in which case it is Hæmatin. Oxyhæmoglobin dissolves readily and without change in very dilute alkaline solutions

* In some instances it is only requisite to dilute the blood and allow one or two drops to dry spontaneously. In others, an abundant crop may be obtained by transmitting air free from carbonic acid through the blood for several hours; or the blood after being defibrinated may be frozen (Rollett's plan) and allowed slowly to thaw; or (Böttcher's method) a considerable quantity of cold water may be injected into the veins of the animal whilst it is being killed by chloroform inhalation, the blood removed rom the heart mixed with its own volume of cold water and some alcohol added, when the whole mass changes into a crystalline pap; or (Kühne's and Thiry's plan) the blood left after the formation of a clot is mingled with some 0·5 per cent. aqueous solution of crystallized ox-bile (tauro- and glycocholate of soda) and then with alcohol (90 per cent.) containing a little acetic acid. The method given by Preyer as the best adapted for microscopical investigation is that to a small quantity of blood free from fibrin, sufficient water should be added to give a clear solution; if on evaporation in the cold a drop of the solution covered by a thin slip of glass give no crystals, about a quarter of its volume of alcohol must be added and the fluid placed in a freezing mixture: crystals will in almost all instances be immediately formed. Speaking generally, in order to obtain blood crystals, the corpuscles must be dissolved, and the colouring matter thrown down by alcohol, or by some salt or acid.

at a low temperature, but strong solutions, or even weak solutions at a moderate or high temperature, effect its decomposition. The solution becomes green in thin layers, brown and dichroic in thick layers, and its spectrum changes. Oxyhæmoglobin readily yields its oxygen to powerful reducing agents, but it is incapable of oxidizing grape-sugar, uric acid, or fat. It possesses in a high degree the power of converting oxygen into Ozone. Hæmoglobin—*i.e.*, reduced oxyhæmoglobin, is much more soluble in water than oxyhæmoglobin, and crystallizes with difficulty or not at all. Professor Ray Lankester* has shown that oxyhæmoglobin is present in the *plasma* of the vascular fluid of various Invertebrata as in that of the Annelids Lumbricus, Eunice sanguinea and Hirudo, in that of the crustacean phyllopod, Cheirocephalus diaphanus; in that of Chironomus amongst Insecta and the Planorbis amongst Mollusca.

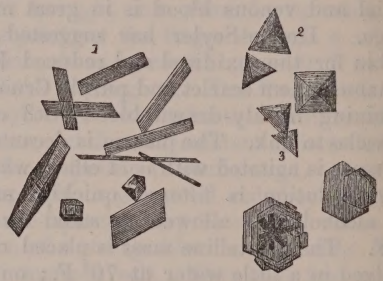
177. Oxyhæmoglobin crystals are obtained with the greatest facility from

FIG. 111.



Spontaneous changes in form of Red corpuscles of Guinea-Pig's Blood, within an hour after removal from the body.

FIG. 112.



Blood-Crystals, (1) prismatic, from Human blood, (2) tetrahedral, from Pig's blood, (3) hexagonal plates, from Squirrel's blood.

the blood of the dog, cat, horse, rat, guinea-pig, squirrel, and goose, less easily from the blood of man, and with the greatest difficulty from the mouse, the mole, and the bat.† Some of the chief forms of oxyhæmoglobin crystals are exhibited in the Figs. 111, 112. It has been ascertained that with the exception of those of the squirrel, which are hexagonal, the crystals of the blood of other animals belong to the rhombic system. Those of man present the form of elongated rectangles, rhombs, and four-sided prisms, with dihedral summits. The crystals of the blood of the rabbit are very similar to those of man. Those of the dog are long four-sided needles, terminated by one plane surface. From cat's blood similar crystals may be obtained, together with thin rhombic and six-sided plates. In the guinea-pig tetrahedra, and in the rat tetrahedra and octahedra are found. Oxyhæmoglobin crystals from whatever animal they may be obtained are always perfectly transparent, and doubly refracting with silky lustre; the crystals of reduced hæmoglobin are pleochromatic, alternating from red or purple to green; but those of oxyhæmoglobin are not so, presenting the colour of the blood from which they are got. When fresh they are soft and highly elastic, breaking with an uneven splintery fracture; exposed to the action of water they imbibe it and undergo various changes of form, never, however, assuming that of a red blood-corpuscle. They contain from 3 to 9 per cent. of water of crystallization. The sp. gr. of oxyhæmoglobin probably varies from 1·3 to 1·4. All the varieties are soluble in

* "Journal of Anat. and Physiology," 1868, p. 114, and 1871, p. 122, and "Proceed. of Roy. Soc.," 1872, Dec. 12th.

† Hoppe-Seyler, "Med.-Chem. Untersuch.," 1867, p. 174.

water, and the solubility increases with the temperature. They are insoluble in absolute alcohol, ether, in volatile and fixed oils, benzol, turpentine, chloroform, and carbon disulphide. They dissolve readily and for some time without undergoing decomposition in the alkalies and most alkaline salts (carbonates, phosphates, borates), but in a few days the solution becomes cloudy from decomposition. Solutions of most acids quickly dissolve them, but decomposition sets in in the course of a few hours. They remain long unchanged in healthy urine, in saccharine solutions, in bile, and serous transudates. Hæmoglobin, though a crystalline compound, is scarcely diffusible, and when pure is not fibrino-plastic. The per-centage composition of hæmoglobin obtained from the dog is C 53·85, H 7·32, N 16·17, Fe 0·43, S 0·39, O 21·84. The amount of oxygen that is taken up by one gramme (15·432 grains) of Hæmoglobin is 1·16 c.c.*

178. *Methæmoglobin* results from the action of any oxidizing substance on oxyhæmoglobin. It is intermediate, in regard to the amount of oxygen it contains, between Hæmoglobin and Oxyhæmoglobin. It is found in old extravasations of blood, and in the blood after the respiration of Amyl-nitrite, and even in the red blood-corpuscles of the living animal.† It is amorphous, very easily soluble in water, insoluble in alcohol and ether. It is converted by acids and alkalies in the absence of oxygen into albumin and hæmatin, and by reducing substances in neutral or weakly alkaline solutions into Hæmoglobin. Its spectroscopic characters are shown in Fig. 115, No. 5.

Hæmatin is obtained by acting on red blood-corpuscles with alcohol containing a little sulphuric acid at a gentle heat; the blackish brown solution obtained owes its colour to hæmatin. It may also be obtained by the extraction of dried and powdered red corpuscles with glacial acetic acid and a little sodium and chloride. Teichmann's *Hæmin* crystals are thus obtained, which have the formula $C_{68}H_{70}N_8Fe_2O_{10}2HCl$. These crystals can be obtained from a very minute speck of blood. They form minute rhombic tablets (Fig. 113), or stellæ of red, brown, or black colour, becoming violet on exposure to oxygen, and losing their transparency on exposure to carbonic acid. They dissolve easily in alkaline solutions, and then on the addition of an acid give a flocculent brown precipitate of hæmatin, $C_{68}H_{70}N_8Fe_2O_{10}$. Hæmatin is insoluble in water, alcohol, ether, and dilute acids, but readily soluble in alkaline solutions. Both acid and alkaline solutions absorb red light up to the line B. They show an absorption band between C and D, and somewhat nearer the former, and a very faint broad band between D and F. Hæmatin withstands without decomposition a temperature of 350° F., but above that point carbonizes.

Fig. 113.

Hæmin Crystals, or Hydrochlorate of Hæmatin (Teichmann) lying in a mass of Sodium Chloride Crystals.

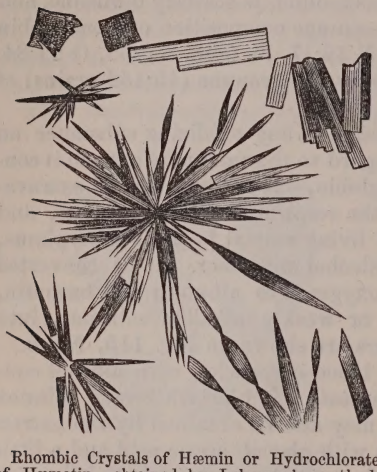
Hæmochromogen, or *reduced Hæmatin.*—This substance was obtained by Stokes by treating solutions of hæmatin with alkaline reducing agents, and it may also be produced by the action of alkalies or acids, or of alcohol, or of a

* G. Hufner, "Zeits. f. Chemie.," 1877, Band i. p. 317. Hoppe-Seyler estimates it theoretically at 1·67 c.c. at 0° C., and 760 m. ("Physiol. Chemie.," 1879, p. 380). Dybkowsky, proceeding on the principle of replacement by CO, found it to be 1·18 c.c. (Hoppe-Seyler, "Med.-Chem. Unters.," Band i. 1866, p. 117). Preyer obtained the numbers 1·37, 1·31, and 1·23 c.c. ("De Hæmoglobino Observat. Diss." Bonn, 1866, p. 19). Strassburg estimated it at 0·885 c.c. (Pflüger's "Archiv," Band iv. p. 454.)

† Hoppe-Seyler, "Phys. Chem.," 1879, p. 391.

temperature of 100° C. in the absence of oxygen on solutions of hæmoglobin.* Hæmochromogen has so powerful an affinity for oxygen that it has not been isolated. Its alkaline solution exposed to oxygen is converted into hæmatin, its colour at the same time undergoing considerable change. Acid hæmochromogen absorbs red and orange, at least as far as the line D, and violet and blue to G. There is an absorption line between D and E, and another at E, which is fainter, and disappears on dilution.

Fig. 114.



Rhombic Crystals of Hæmin or Hydrochlorate of Hæmatin, obtained by Lehmann's method. They are obtained when blood is subjected to the action of a mixture of one part of alcohol, 4 parts of ether, and 1-16th of oxalic acid, and appear as thin brownish and brownish-green, striated, transparent crystalline laminæ, often curiously twisted upon their long axes, and soon spontaneously changing into flat rhombic octahedra.

Hæmatoporphyrin. — The iron-free hæmatin obtained by the action of concentrated sulphuric acid upon hæmatin consists essentially of Hæmatoporphyrin mingled with a substance named *hæmatolin*, which is insoluble in most menstrua, and has a composition expressed by the formula $C_{68}H_{78}N_8O_7$.† Hæmatoporphyrin is soluble in alkaline solutions, and has the composition $C_{68}H_{74}N_8O_{12}$. Its acid solutions present a narrow and feeble absorption band just before the line D, and a darker and broader one between D and E. The alkaline solutions which, like the acid, have a fine purplish hue, exhibit four absorption bands: a narrow one between C and D; a broad and dark one at D, stretching farther towards E than toward C; a narrow, feeble one between D and E, but nearer E; and, lastly, a broad dark one commencing before *b* and extending beyond the middle of the interspace between *b* and F. Considerable interest attaches to this body since it closely resembles hydrobilirubin in its spectrum and in its relation to solvents. When treated with concentrated sulphuric acid, the iron can be wholly withdrawn, and the hæmatoin, or *iron-free hæmatin*, called also *acid-hæmatin*, thus obtained, so far differs from ordinary hæmatin, that whilst it is insoluble in dilute acids, it presents the important chemical feature of being polymeric with bilirubin, or the colouring matter of bile, as shown by the following formulæ:—

$$\underset{\text{Hæmatoin.}}{C_{96}H_{51}N_6Fe_2O_{18}} + 3H_2O = 3(\underset{\text{Bilirubin.}}{C_{32}H_{18}N_2O_6}) + 3FeO$$

Thus, Hæmatin is the substance which contains all the iron of the blood, whilst the Hæmatoin (which, according to Hoppe-Seyler, consists of hæmatoporphyrin and hæmatolin) contains no iron. The *Hæmatoidin* crystals observed by Virchow, and stated by him to occur in blood that has long been extravasated, as in old apoplectic clots, and in corpora lutea, appear to be identical with bilirubin, or the colouring matter of bile. The formation of these crystals takes place with considerable rapidity. If a little coagulated pigeon's blood be introduced beneath the skin of that bird, hæmatoidin crystals appear in the course of two days.‡ The crystals are soluble in ammonia, inso-

* "Proceed. Roy. Soc.," June, 1864. † Hoppe-Seyler, op. cit., 1879, p. 397.

‡ Langhans, quoted in Fehling's "Neues Handwörterbuch der Chemie," 1875, Band ii. p 112.

luble in alcohol and acetic acid. They are acicular, frequently bent, partly grouped into stellæ and doubly refractile. They are insoluble in alcohol, ether, and water; but very soluble in weak solution of potash, or weak acetic acid.*

179. Spectrum Analysis of the Blood.—The researches of Brewster, Herschel, and Müller showed that when solutions of various colouring matters are placed in the solar spectrum, certain portions of the light are absorbed, and dark striæ or bands appear in the spectrum corresponding to those rays that have been arrested. F. Hoppe† found that in a very diluted mixture of blood and water the spectrum exhibited two well-marked dark striæ (2, Fig. 115) in the yellow and in the green, both lying between the Fraunhofer lines, D and E. When less dilute, the two lines blended together, and with increasing concentration, the violet and blue, as well as the green and yellow, gradually vanished, till at length only the red remained. Arterial and venous blood alike showed the two striæ, as did also dried blood, and blood treated with CO_2,CO,H,SH,NH_3, &c.; but the striæ rapidly disappeared when acetic or tartaric acid, or caustic alkaline lyes were added to the blood. He further found that the ordinary absorption striæ were rendered most distinct by precipitating a mixture of blood and water with acetate of lead, and throwing down the lead with carbonate of soda. Prof. Stokes,‡ on repeating the experiments of Hoppe, confirmed them, and at once proceeded to inquire whether it were possible to imitate the change of colour of arterial into that of venous blood, on the supposition that it arose from reduction. This he accomplished by adding solution of protosulphate of iron, with enough tartaric acid to prevent precipitation by alkalies, to the blood, when the colour of the solution immediately became much deeper, and the two absorption bands were at once replaced by a single band (4, Fig. 115) shaded off at the borders, and occupying an intermediate position between them. On exposure to air, the bands originally present reappeared. Hence he inferred that the colouring matter of the blood, like indigo, is capable of existing in two states of oxidation, distinguishable by a difference of colour and a fundamental difference in the action on the spectrum. To this colouring-matter he has applied the term Cruorin, suggested by Dr. Sharpey—its two states of oxidation being termed scarlet cruorin, and purple cruorin respectively. Prof. Stokes showed also that hæmatin, which is the result of the action of weak acids on cruorin, was similarly capable of oxidation and reduction, and that it shows well-defined and highly-characteristic lines, which, however, are by no means identical with those of cruorin. Prof. Stokes suggests, as a physiological deduction from his experiments, that cruorin is to be regarded as the carrier of oxygen to the tissues, since it absorbs that gas with extreme facility; whilst under the influence of reducing agents it permits it again to be withdrawn from it. Both Hoppe and Stokes refer to the applicability of spectrum analysis for the detection of blood-stains in medico-

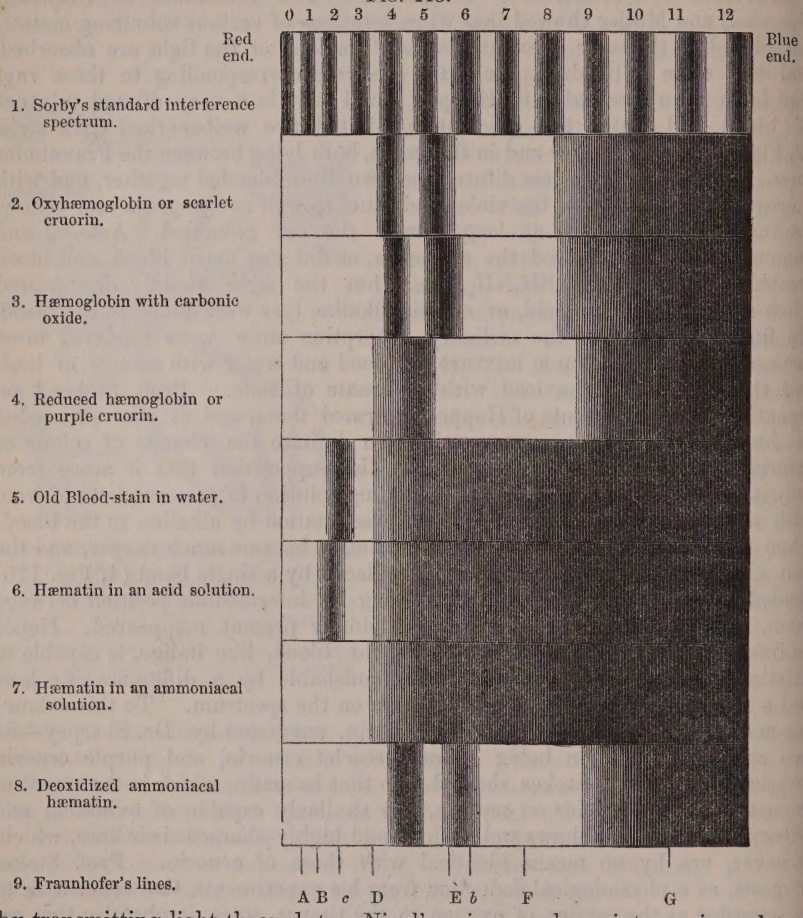
* For the best accounts of the crystals of blood, see Teichmann, "Zeitschrift f. Rat. Med.," N. F. iii. 375, viii. 141; Kölliker, "Manual of Human Histology," 1860; Virchow, "Cellular Pathology," 1860, pp. 143–145; v. Gorup-Besanez, "Phys. Chem.," 1862, pp. 170–194; Funke, "Physiologie," 4th edit. 1863, p. 45; Bojanowski, Siebold, and Kölliker's 'Zeitschrift," Band xii. 1862, p. 312; Rollett, Moleschott's "Untersuchung," 1863, p. 22; Böttcher, Virchow's "Archiv," 1865, p. 126 and p. 372; Zawarykin, "Sitzungsberichte d. k. Akad. zu Wien," 1865, p. 151; Gwosdew, idem., 1866; Hoppe-Seyler, "Med.-Chem. Untersuch.," 1867, p. 298; Kühne, "Physiolog. Chemie," 1868, p. 188, *et seq.*; Thudichum, 'Centralblatt," 1869, p. 1; Preyer, "Die Blutkrystalle," Jena, 1871, which last contains all the references up to that date, and gives the fullest account yet published.

† Virchow's "Archiv," Band xxiii. 1862, p. 446.

‡ "Proceed. Roy. Soc.," vol. xiii. 1863–64, p. 355.

legal investigations. Mr. Sorby* has greatly improved the mechanical arrangements by which the lines in question can be examined, and the adjoining woodcut, Fig. 115, is after a drawing by his hand. The uppermost scale represents Mr. Sorby's standard interference spectrum, and is obtained

Fig. 115.


0 1 2 3 4 5 6 7 8 9 10 11 12
Red end.
Blue end.
1. Sorby's standard interference spectrum.
2. Oxyhæmoglobin or scarlet cruorin.
3. Hæmoglobin with carbonic oxide.
4. Reduced hæmoglobin or purple cruorin.
5. Old Blood-stain in water.
6. Hæmatin in an acid solution.
7. Hæmatin in an ammoniacal solution.
8. Deoxidized ammoniacal hæmatin.
9. Fraunhofer's lines.
A B c D E b F G

by transmitting light through two Nicol's prisms and an intervening plate of quartz or selenite, with its axis at 45° to the plane of polarization. The number of the dark bands due to the interference of the luminous waves may be regulated by the thickness of the plate of quartz, and for the sake of convenience has been fixed at 12, the unequal dispersion making the distance between the bands in the blue about twice as great as in the red. The dark bands are numbered 1, 2, 3, 4, &c., and the centre of the white spaces $1\frac{1}{2}$, $2\frac{1}{2}$, $3\frac{1}{2}$, &c., which may be again subdivided, as into $1\frac{1}{4}$, $1\frac{3}{4}$, &c. Definite narrow absorption bands are indicated by an asterisk printed over their centre. On this notation the bands occurring in the several solutions mentioned may be described intelligibly and simply thus:—

* "Quart. Journ. of Sci.," 1865, vol. ii. p. 198; "Pop. Sci. Review," vol. v. p. 66; "Proceed. of Roy. Soc.," vol. xv. 1866–7, p. 433. For an account of Vierordt's method of notation see Dalton "N.Y. Med. Journ.," vol. xix. 1874, p. 579.

2. Oxidized hæmoglobin . . .	$3\frac{5}{8}$—$4\frac{3}{8}$	$4\frac{3}{4}$—$5\frac{3}{4}$	8— 9—
3. Hæmoglobin with CO . . .	$3\frac{3}{4}$—$4\frac{1}{2}$	$4\frac{7}{8}$—$5\frac{7}{8}$	8— 9— and so on.

According to Mr. Gamgee,* the nitrites cause blood to assume a chocolate colour, the bands of oxidized hæmoglobin becoming very faint, and an additional absorption band in the same position as in acid hæmatin (6, Fig. 115) appearing. The nitrites do not decompose the blood-colouring matter, nor discharge the oxygen. They appear to link themselves on to it, as is probably the case with hydrocyanic acid.† Nitritized blood absorbs less oxygen, but it can convert into ozone what it does absorb. On exposure of oxyhæmoglobin to carbonic oxide gas, combination takes place, and a comparatively stable compound is formed; the solution assumes a clear cherry-red colour, and the spectrum presents two striæ, which lie rather closer together than those of oxyhæmoglobin, and are shifted a little towards the violet end of the spectrum. These do not fuse into one on the application of reducing agents, as happens with oxyhæmoglobin. If breathed, carbonic oxide proves fatal by replacing the oxygen in the blood-corpuscles and preventing the absorption of that gas.

180. There can be no doubt that both the red and the colourless corpuscles have, like other cells, a definite term of life; and that, whilst some are undergoing disintegration, others are in a state of advancing development to supply their places, so that the entire mass of both is undergoing continual change. That a new production of red corpuscles may take place with considerable rapidity, we have evidence in the rapid restoration of their normal proportion after it has been lowered by hæmorrhage, and in the speedy increase which may be effected in their amount in blood in which they have been excessively diminished by disease, this being especially promoted by the administration of iron, and by a generous diet. On the other hand, various appearances indicative of degeneration may be seen in the red corpuscles; and this especially in the blood of the Oviparous Vertebrata, which usually contains corpuscles almost destitute of colour, and having a shrunken or eroded aspect—their nuclei, however, presenting a remarkable distinctness. That, under certain circumstances, such a degenerating process takes place with great rapidity in the blood which circulates through the Spleen, may be considered as ascertained almost beyond a doubt (§ 157, III.). The duration of the individual corpuscles is unknown, the only evidence yet obtained being derived from the experiments of Bernard, who found that when the blood of birds was injected into the vessels of mammals, the elliptical corpuscles of the former, which were at first plainly visible, disappeared entirely in the course of a few weeks. The question now arises, in what manner the two classes of corpuscles are respectively developed, and whether they have any relationship to each other.

181. Coagulation of the Blood.—When the Blood has been drawn from the body, and is allowed to remain at rest, it undergoes at ordinary temperatures spontaneous coagulation, forming at first a solid mass of jelly-like consistency, of the same bulk as the liquid blood. After a time a few drops of a transparent fluid appear upon the surface of this mass; the amount of this liquid gradually increases, whilst the red solid mass—the crassamentum, or clot, as it is called—as gradually shrinks till at length the clot floats in the nearly colourless liquid or serum. The clot is composed of a network of Fibrin, presenting a more or less distinct fibrous texture; in the meshes of which the Corpuscles, both red and colourless, are involved, together with a certain amount of serous fluid, and

* "Proceedings of Roy. Soc.," No. 102, 1868.

† Preyer, Virchow's "Archiv," Band xl. 1867; and Hoppe-Seyler, "Untersuch.," 1867.

it is to the formation of this network of fibrils due to the development of fibrin in the plasma that the clot owes its origin. The serum, which is the same with the liquor sanguinis deprived of its fibrin factors, coagulates by heat, and is therefore known to contain Albumin; and if it be exposed to a high temperature sufficient to decompose the animal matter, a considerable quantity of earthy and alkaline Salts remains.—Thus, we have four principal components in the Blood: namely, *Fibrin factors*, *Albumin*, *Corpuscles*, and *Saline matter*. In the *circulating* blood, they are thus combined:—

Fibrin factors, Albumin, Salts } In solution, forming Liquor Sanguinis.
Corpuscles,—suspended in Liquor Sanguinis.

But in *coagulated* blood they are combined as follows:—

Fibrin, Corpuscles } Forming Crassamentum, or Clot, which, however, always contains more or less serum in its meshes.
Albumin, Salts } Remaining in solution, forming Serum.

The *coagulation of blood* consists in the new arrangement of its constituents, which takes place when it is drawn from the vessels, or when the body itself dies. This new arrangement essentially depends upon the conversion of a substance called plasmin into fibrin. The plasmin does not exist as such in the blood, but is formed by the interaction of two substances, fibrin and fibrino-plastin, under the influence of a ferment. These bodies will be considered in greater detail below. The clot which is thus formed is not an amorphous coagulum, but is a network of fibres more or less definitely marked out, in the meshes of which network are included the red corpuscles usually grouped together in columnar masses resembling piles of coins. The *crassamentum*, or clot, gradually acquires a firmness proportioned to the amount of fibrin which it contains and to the degree of its elaboration, and then undergoes a progressive contraction, by which the albuminous, saline, and extractive matters still in solution are more or less completely expelled from it, constituting the *Serum*. This separation will not occur, however, if the coagulation takes place in a shallow vessel, nor if the amount of fibrin happens to be small. Under such circumstances a homogeneous mass, deficient in firmness, presents itself, though the solid parts of this may pass into a state of more complete condensation after the lapse of a certain time. That the coagulation is due to the fibrin, and that the red corpuscles do not take any active share in the process, appears from several considerations.* The corpuscles, being of greater specific gravity than the plasma, or liquor sanguinis, will sink to the bottom of the vessel in which the blood is contained, provided that it is left undisturbed. Under ordinary circumstances the rapid clotting of the blood prevents this subsidence. If, however, the blood of a mammal—the horse, for example—be received into a vessel placed in a freezing mixture, and is thus kept at a

* For an admirable summary of the history of opinions in regard to the subject of blood coagulation, see the Introduction to the works of William Hewson, F.R.S., by George Gulliver, F.R.S., London, printed for the Sydenham Society, 1846. Also for experiments in regard to the coagulation o the blood, Dr. Andrew Buchanan, "Lond. Med. Gazette," vol. xviii. 1836, p. 50; and vol. i. (New Series, 1845), p. 617. The latter paper is reprinted in the "Journal of Physiology," vol. ii. p. 158, 1879. An account of Dr. Buchanan's work is also to be found in "The Natural History Review," vol. iv. 1864, pp. 157–187; and further mention of him with additional experiments by Prof. Gamgee in the "Journal of Physiology," vol. ii. 1879, pp. 145–157.

temperature below 0° C., it will not coagulate, and the corpuscles will therefore be enabled to subside. When this has taken place, the liquor sanguinis may be decanted off, and will be found to coagulate in a perfectly normal manner, the clot being colourless, and containing no red corpuscles, but a number of white ones, entangled in the mesh-work of fibrils. The same experiment may be performed by adding to the blood about one-third of its bulk of a saturated solution of certain neutral salts, such as sulphate of soda or magnesia, or carbonate of potash, which have the property of retarding coagulation. Similar results are obtained by observations on the so-called "buffy coat," which occurs in certain disorders of the blood. This coat is a layer, nearly free from colour, which is found on the surface of the clot. Its presence has been frequently regarded as a sign of the existence of inflammation, indicating an undue predominance of fibrin; but this idea is far from being correct, since, as occurs in chlorosis, it may result from an opposite condition of the blood. Its occurrence in the human subject, excepting in the female during the later stages of utero-gestation, is certainly pathological; but in some animals, as in the horse, the blood-clot is ordinarily buffy. The appearance of this buffy coat in the horse is perhaps to be explained by Cl. Bernard's observation, which shows that even during life the blood-cells gravitate to the lowest parts of the fluid. In a horse laid out on the ground in such a position that its long jugular vein was nearly horizontal, a small opening made in the upper surface allowed the escape only of the plasma, without red corpuscles, whilst from a similar small opening made at the lowest surface of the vein some very black blood issued. Both portions coagulated; the first, of course, giving a colourless clot; the second, as usual, a dark clot, with a well-marked buffy coat.* The buffy coat, then, is due to the clumping together, and consequent more rapid sinking, of the red corpuscles, and this is further shown by the fact that its appearance is hindered by artificially separating the corpuscles, whilst it is hastened or increased as their aggregation increases. Thus, as has been already mentioned, and as Mr. Gulliver has shown, solutions of neutral alkaline salts prevent the running together of the corpuscles, and retard the formation of the buffy coat. On the contrary, certain viscid matters facilitate the clumping of the corpuscles, and coincidently the quickness of the formation and the quantity of the buffy coat. Mr. Gulliver has also noticed that in fluid blood the sinking of the red corpuscles increases in a kind of arithmetical ratio, being slowest when they first begin to collect into clumps, and more rapid at the very time when these clumps are most fully formed; so that the corpuscles would in some instances take two and a half minutes at first to sink through one-eighth of an inch of liquor sanguinis; but only two and a half minutes more to sink through a further three-eighths of an inch. It is remarkable, as Gulliver† notices, that Hunter was well acquainted with the clumps of red corpuscles in inflammatory blood. The evidence is therefore satisfactory which tends to show that the red blood-corpuscles have no influence upon the cogulation of blood.

182. The influence of Fibrin upon the process of coagulation is shown by whipping the blood with a bundle of twigs, or by stirring it with a stick, when the fibrin will adhere in strings during its coagulation; and the red corpuscles will be left suspended in the serum, without the slightest tendency to coagulate. The actual cause of the separation and coagulation of the fibrin is still obscure. Dr. Buchanan‡ remarked long ago that fibrin might apparently be

* Bernard, "Leçons," 1859, p. 432.

† Lectures, "Med. Times and Gaz.," Oct. 17, 1863; Hewson's works.

‡ "Proc. Glasgow Phil. Soc.," 1845, and loc. cit.

formed, or at least that coagulation could be induced, by mixing two serous fluids like those of Hydrocele and Ascites, or of Ascites and Pleurisy, neither of which had separately any tendency to coagulate; and that coagulation was equally caused by putting into the serum portions of blood-clot, or of fibrin, either fresh or powdered, muscular fibres or other tissues. Schmidt,* in more recent observations, attempts to explain the phenomena in question by attributing them, as already mentioned, to the combination of two substances existing in the liquor sanguinis under the influence of a ferment which is rapidly formed in the blood after its removal from the body. To one of these bodies, which is contained in considerable quantity in the blood, he has given the name of Fibrino-plastin, Globulin or Crystallin, though it differs from the crystallin obtained from the lens of the eye in its non-precipitability by heat and alcohol, and has therefore been termed by Kühne Paraglobulin. It is precipitated when its alkaline solution is exactly neutralized, and is obtained from blood or other tissue which contains it, such as connective-tissue, cornea, &c., by the passage of a continuous current of carbonic acid through the greatly diluted fluid, or by saturation with one of the neutral salts which were mentioned above as retarding coagulation like common salt. The precipitate of fibrino-plastin thus obtained is at first flocculent, then granular; it is insoluble in distilled water, and is more readily isolated than Fibrinogen, the second substance which is closely allied to albumin. Fibrinogen differs from fibrino-plastin in the circumstance that its alkaline solution must be rendered acid before precipitation occurs. It is found chiefly in the plasma and in such exudations as hydrocele fluid. As ordinarily prepared, it is a viscid substance. Both Schmidt and Hoppe-Seyler have been successful in producing a coagulum differing in no respect from ordinary fibrin, by the admixture of these two substances prepared in one of the above ways. Mr. Goodman† has pointed out that ovalbumin suspended for some time in cold and pure water loses the character of albumin, and assumes the nature, appearance, and constitution of Fibrin; and he accounts for the formation of the fibrin of the blood in this way. The general explanation put forward by Schmidt in regard to the cause of the coagulation of blood is perhaps the best that can be at present offered. Plasmin, a substance discovered in blood which has been kept from clotting by artificial means, by Denis,‡ can be precipitated by

* Müller's "Archiv," 1862, p. 543. See also Mantegazza, "Annali Universali di Medicina," t. ccxvi. April, 1871. In opposition to Schmidt, see Eichwald, "Beiträge zur Chemie der gewebe-bildenden Substanzen und ihren Abkömmlinge," 1873. Eichwald regards the Fibrin as being normally dissolved in the plasma, but undergoing precipitation when exposed to the action of the carbonic acid of the air. Denis divides the Albuminous compounds of the blood into *Serin* (amounting to 52 parts per 1000 of blood), which is coagulable by heat and acids; and *Plasmin* (25 per 1000), which is precipitated by NaCl, but redissolves in from 10–20 parts of water. The plasmin is capable of breaking up spontaneously into concrete fibrin (3–4 per 1000) and soluble fibrin (22 per 1000), the proportions of which bear an inverse ratio to each other. Hence, as Sée maintains, it is never a question in disease of excess or defect of fibrin, but simply of the relative proportions of the concrete and soluble fibrin. See Küss, "Physiologie," 1873, p. 158, and Budge's "Compendium de Physiologie," 1874, p. 260. "Handbook for the Physiological Laboratory," London, 1873, p. 173; Alex. Schmidt (i.) "Neue Untersuchungen über die Faserstoffgerinnung," Pflüger's "Archiv," vi. 1872, pp. 413–538; (ii.) "Ueber die Beziehung der Faserstoffgerinnung zu den körperlichen Elementen des blutes;" Pflüger's "Archiv," xi. 1875, pp. 291–369 and 515–577; (iii.) "Die Lehre von der fermentiven Gerinnungserscheinungen in der eiweissartigen thierischer Körperflussigheiten," Dorpat, 1876; Burdon Sanderson, 'Lectures on the Infective Processes of Disease,' "British Med. Journ.," vol. i. 1878, p. 119; Foster, "A Textbook of Physiology," ed. ii. pp. 25–27.

† "Fibrin: its Origin and Sources of Development," Pamphlet, 1871, p. 12.

‡ "Ann. d. Sci. Nat.," iv. p. 25.

saturation with neutral salts, and is formed by the union of fibrinogen and fibrino-plastin. The union of these two substances is brought about by means of a ferment, that is to say, of a body which by its presence excites chemical action without itself taking part in it. The plasmin thus produced passes very readily into fibrin.*

183. That the union of fibrinogen and fibrino-plastin in the blood is brought about by means of a *ferment* is still an hypothesis, the train of reasoning, however, which has led investigators to adopt this theory is somewhat as follows:†—If the chest of a large mammal be opened immediately after death, it will be found that the fluid removed from the pericardium clots rapidly. If the opening, however, be deferred for 20 or more hours, the pericardial fluid will be found either not to coagulate at all or to coagulate very slowly and feebly. The addition of fibrino-plastin, however, effects a rapid and copious coagulation. Again, if, as Kühne‡ states, three parts of plasma be mixed with one part of a solution of magnesium sulphate, containing one part of the salt to 3·5 of water, and the whole be diluted with eight parts of water, it will be found that little or no coagulation occurs, although an excess of fibrino-plastin is present. The addition of paraglobulin to such a solution causes rapid coagulation; moreover, fibrinogen and fibrino-plastin prepared by the carbonic acid§ method, clot much less readily in a saline solution than when prepared by saturation‖ with a neutral salt. A watery extract of blood is readily obtained by pouring blood into a large excess of alcohol; it must not be allowed to flow into the alcohol directly from the artery, otherwise, according to Hermann, the desired result is not obtained. It is allowed to remain for some weeks below the alcohol, to precipitate all the proteid matters. The spirit is then decanted and evaporated off, and the residue, after being dried at a temperature below 40° C., is extracted with water. An aqueous solution of the alcoholic precipitate is thus obtained, which contains substances dissolved or suspended in it which, though soluble in water, are insoluble in alcohol. This extract gives only very slight proteid reactions; if, however, a small quantity of it be added to the plasma mentioned in the second experiment, or to some of the pericardial fluid, coagulation rapidly occurs. In the aqueous solution there is present some principle which is capable of causing coagulation in fluids containing both fibrinogen and paraglobulin (fibrino-plastin), though it does not do so in those cases where there is reason to suppose that only one of these bodies is present. It is this principle which is known as the ferment, and it belongs to that class of ferments known as unorganized, to which allusion has already been made (§ 68). This ferment effects coagulation only in relation to the rapidity with which that phenomenon sets in, for if a larger quantity of the aqueous extract be added it will be found that coagulation sets in more quickly, though there is no increase in the amount of the clot; consequently the ferment is essential to the union, or at least interaction of the two fibrin factors, though it does not contribute to the formation of the clot. The question then arises, where is this ferment in the normal condition of the blood? Undoubtedly it is not usually present. Hermann observes that it

* Prof. Schmidt is doubtful as to whether fibrin is formed by the actual union of fibrinogen and fibrino-plastin; it is therefore better to leave this point open, and to state that fibrin originates by the interaction of fibrinogen and fibrino-plastin, under the influence of a ferment.

† Foster, "Physiology," ed. ii. p. 19.

‡ "Lehrb. der Physiol. Chem." p. 172.

§ "Handbook for Physiol. Lab.," p. 170, obs. 2 and 3.

‖ "Handbook," p. 171, obs. 10.

is developed only at the death of the blood, hence his caution in preparing the alcoholic extract, against allowing the blood to flow directly from the vessel into the alcohol.

184. As Mantegazza* has observed, the presence of white blood-corpuscles is necessary for coagulation; since it is well known that a clot is formed wherever the endothelium of a vein is irritated so as to undergo germination. The observations of Mantegazza are abundantly confirmed by facts: thus, to take a few cases. It is found that if the red blood-corpuscles be removed as completely as possible by subsidence and decantation under the circumstances already described (§ 181), and be added to a quantity of serum which is equivalent to the amount of blood from which they were removed, the serum will clot. This coagulation, however, is not due to any influence exercised by the red blood-corpuscles, as has already been shown. Again, Müller placed the blood of a frog diluted with water, or still better 0·75 per cent. sodium chloride solution, on a paper filter. The plasma passed through completely unmixed with red corpuscles, but it presented a distinct coagulum, although from the diluted state of the fluid this did not possess much consistency. In this experiment it is found that the white corpuscles, from their extreme lability pass through the filter at the ordinary temperature,† and that it is only when the whole operation is conducted at a temperature of 0° C. that the white corpuscles can be filtered off. When this precaution has been taken and the white corpuscles have been separated, the plasma refuses to clot, though it does so on addition of the white corpuscles. The lymph from blisters, which contains no red corpuscles, but numerous white ones, coagulates normally. Schmidt‡ also gives the following experiment as being a good example of the influence of the white corpuscles on the coagulation of the blood:—The blood is allowed to flow into a deep vessel which is surrounded with ice to retard coagulation, the red blood-corpuscles subside, and a clear stratum is left which contains many white corpuscles. The clear stratum is carefully decanted on to an ordinary filter-paper, which is also kept at a freezing temperature. A transparent filtrate free from white corpuscles is thus obtained. This filtrate has lost its power of coagulation, since the liquid may be kept for several hours in a room at the ordinary temperature. The colourless corpuscles may be freed from any adherent plasma by washing with ice-cold water. The white corpuscles are then broken up by pouring on to them a little water rendered slightly alkaline with sodium carbonate, when a solution passes through which causes immediate coagulation. Brown-Séquard§ has made the curious observation that on injecting defibrinated blood into the separated limbs of animals, fibrin is formed, especially if the muscles are tetanized: similar results have also been obtained by Bernard.‖ It is remarkable, moreover, that splenic venous blood, which contains an excess of white corpuscles, when defibrinated will on exposure to the air form a second coagulum. Professor Schmidt, of Dorpat, whose investi-

* Mantegazza (Moleschott's "Untersuch. zur Naturlehre" Band xi. p. 523; "Centralblatt," 1877, p. 23) has recently advanced a theory of coagulation, in which he regards it as an expression of vitality, instead of, as Schmidt regards it, a phenomenon associated with the death of the blood. Mantegazza looks upon it as a phenomenon of reaction of the white corpuscles to some stimulus usually of a foreign body, or some roughness of the internal coats of the vessels; at any rate, if any such roughness exist it is quickly covered with white corpuscles and fibrin, whilst no fluid coagulates unless it contains white corpuscles. Beltrami thought that fibrin was the detritus of muscular substance, and Lussana adopted this view because he found more fibrin in the blood of tetanized animals, but Mantegazza, on the other hand, observed a diminution rather than an increase.

† Burdon Sanderson, loc. cit., vol. i. 1878, p. 46.

‡ Schmidt, op. cit., p. 47.

§ "Journ. de la Physiol." t. i. p. 299, 1858.

‖ "Leçons," 1859, vol. i. p. 460.

gations have been mentioned above,* has published the results of his many years' laborious researches upon this subject, and he, too, has come to the conclusion that the colourless corpuscles of the blood exert a very material influence upon the coagulation of that fluid. He has noticed that previous to the occurrence of coagulation in the blood a certain number of the leucocytes undergo disintegration. From this breaking up that ferment probably proceeds which causes the fibrino-plastin to interact with the fibrinogen in such a way as to produce the substance known as Fibrin; or, in other words, the blood ferment is contained within the white blood-corpuscles. Professor Schmidt† bases his theory essentially upon the fact that if freshly-drawn blood be examined without delay, the white corpuscles may be seen to break up into granules; these granules for a time cohere in the liquid, but they eventually dissolve and disappear; whilst from the heaps of granules thus formed, and more particularly from those which belong to the transitional forms of white corpuscles containing coloured particles, the first-formed filaments of fibrin can be seen to originate.

185. The theory of a ferment present in the white blood-corpuscles, which is set free on their disintegration, explains a great number of facts in regard to the coagulation of blood. Still it must be remembered that it is as yet but a theory, which has to be proved by facts. Upon this assumption the caution given by Hermann is to be explained, for he recommends, as before stated (§ 183), that blood should be allowed to flow into an intermediate vessel, and not directly into strong alcohol, for by this means the disintegration of the white corpuscles is to a considerable extent insured; whereas, if the blood passed directly from the vessels into an excess of alcohol, the white corpuscles might be so hardened that little or no ferment would be liberated. An explanation is likewise afforded of the fact that the fibrillation is the more perfect the more slowly it takes place; that the coagulation of such blood as is met with in conditions of acute inflammation, which produces a clot of remarkable firmness, is much longer in taking place than the coagulation of ordinary blood; whereas the blood of cachectic subjects, which clots very rapidly, is feeble and imperfect. The plastic effusions poured out from the blood in these two opposite conditions partake of the character of the blood itself; those of the inflammatory blood of a previously healthy subject being converted into fibrous membranes of considerable firmness, which are subsequently penetrated by blood-vessels, and become regularly organized tissues. Those, on the other hand, which proceed from the blood of cachectic subjects frequently undergo a degree of organization with great rapidity, but do not attain the same perfection, and speedily degenerate.‡ Further, that the contact of a dead substance promotes coagulation,§ even in the living and actively moving blood, is shown by the experiment first performed by Mr. Simon, of carrying a single thread transversely (by means of a very fine needle) through an adjacent artery and vein in a dog. The thread is allowed to remain in position for a period of from twelve to twenty-four hours, when a coagulum is formed which more or less completely obstructs the vessel; whilst the thread itself is found on examination to be covered with colourless corpuscles. In such experiments there is a marked difference between the coagula formed in

* "Die Lehre von der fermentativen Gerinnungserscheinungen in der Eiweissartigen thierischer Körperflussigkeiten," Dorpat, 1876.

† Pflüger's "Archiv," 1875, p. 560.

‡ Mr. Dalrymple's Memoirs 'On the Rapid Organization of Lymph in Cachexia,' in the "Med.-Chir. Trans.," vol. xxiii.; and 'On the Early Organization of Coagula and Mixed Fibrinous Effusions under certain Conditions of the System,' op. cit. vol. xxvii.

§ Lister, 'Croomian Lect.,' "Lancet," 1863, vol. ii. p. 179.

the artery and those formed in the vein, which may be attributed to the difference in the rate of the blood-current. The thread which traversed the artery usually presents a "vegetation" on its surface, sometimes as large as a grain of wheat, always of a pyramidal shape, with its base attached to the thread, and its apex down stream. The venous coagulum is a voluminous black clot, chiefly collected on that side of the thread which is most remote from the heart.* The explanation of this is to be found in the fact that injury to the endothelium lining of the vessels causes a germination or proliferation of white corpuscles, some of which becoming broken up liberate the ferment. That this is the case is shown by the fact that blood which has been allowed to coagulate, and has been strained from the clot, acts as a rapid poison when re-injected into the arteries of the animal from which it was taken; the cause of death in such a case being embolism in the capillaries.† M. Dupuy, and afterwards M. de Blainville, in like manner found that the injection of cerebral substance into the veins of an animal occasioned its death almost as instantaneously as if prussic acid had been administered; the circulation, as in the case after the injection of cruorin in the previous experiment, being rapidly brought to a stand by the formation of voluminous clots in the heart and large vessels.‡ There is no reason to suppose that cerebral substance possesses a more special influence than would be exerted by any other tissue which could be as easily mixed up with the circulating current, for in both cases the presence of the injected fluids suffices to determine coagulation in blood in which it would not otherwise have occurred. The same effect is produced with still more potency when the substance injected is rather undergoing degradation than actually dead, as is well observed in the case of pus, noticed originally by Hunter and afterwards by Mr. H. Lee. Healthy blood received into a cup containing some offensive pus coagulated in two minutes; whilst another sample of the same blood received into a clean vessel of similar size and shape required fifteen minutes for its complete coagulation. Mr. Lee found that when pus was injected into the jugular vein of a living ass, coagulation took place so instantaneously as to produce an immediate obstruction to the current of blood, so that the vessel at once acquired a cord-like character; and in this mode the pus was usually prevented from finding its way into the general current of the circulation. Whilst it thus remains circumscribed by a coagulum of blood, the pus so introduced seems to produce no other constitutional disturbance than is attributable to the local injury; but if the circumscription should be incomplete, and the pus should be carried into the general circulation, it becomes a source of extensive mischief, determining the formation of abscesses in various parts, and producing a most depressing influence on the system at large.§ These facts are explicable, as in the case of the injection of cruorin or filtered blood-clot, by assuming that the white corpuscles break up under certain influences, and set free a ferment which in presence of the two fibrin factors, fibrinogen and fibrino-plastin, causes them to interact in such a way as to form plasmin, which in turn is converted into fibrin. In like manner may be explained the observation that when the coagulum of blood from which the fibrin has been removed by whipping, is frozen and allowed to thaw again, a further coagulum is obtained, because some of the white corpuscles which had escaped disintegration in the first instance are then broken up, and a fresh supply of ferment is liberated. As also Mr.

* "Lectures on General Pathology," p. 56; Brücke, "Vorlesungen," 1874, p. 81, *et seqq.*

† Burdon Sanderson, op. cit., vol. ii. 1877, p. 913, *et seqq.*; and vol. i. 1878, pp. 45 and 46.

‡ "Gaz. Med.," 1834, p. 521.

§ "On the Origin of Inflammation of the Veins and Purulent Deposits."

Thackrah's* experiments, that coagulation occurs more rapidly in rough vessels than in smooth, and in metallic than in those of glass and earthenware, since there is less disintegration of white corpuscles in the former than in the latter. Mr. Thackrah found that the quantity of serum separated from blood-clotting in metallic vessels is much less than that obtained from a similar coagulum in an earthenware vessel; thus, in one instance the proportion was as 10 to 24·5 when the blood coagulated in a glass vessel, whilst a portion of the same blood coagulating in a pewter vessel gave only 10 of serum to 175 of clot. The specific gravity of blood is no measure of its coagulating power; for a high specific gravity may be due to an excess in the amount of corpuscles which form the heaviest part of the blood, and may be accompanied by a diminution of the fibrin factors, which are the coagulating elements.

The ferment theory which is here adopted does not, however, explain all the phenomena of the blood coagulation, for it is found that blood returning from the kidneys and liver has little or no tendency to coagulate, in spite of the fact that like the blood of the splenic vein an excess of white corpuscles is found in the renal and hepatic veins. In the same way, no explanation is afforded of the fact that the hearts of cold-blooded animals may be kept full of blood for several days after removal from the body without the occurrence of coagulation; nor is Lister's† experiment explained, in which the jugular vein is ligatured at the bottom and a piece of it is excised, this portion being filled with blood, no coagulation takes place for a long period, and blood may be poured from one preparation‡ to a second without coagulation occurring. So also the observation of Schroeder van der Kolk§ that if the substance of the brain and spinal marrow be destroyed coagulation of the blood takes place whilst it is still moving in the vessels, clots being found in them even within a few minutes of the operation, is still left without explanation.

186. Instances occasionally present themselves, in which the blood does not coagulate after death, or coagulates very imperfectly. It was affirmed by Hunter‖ that no coagulation occurs in the blood of animals hunted to death, or of those killed by lightning, by electric shocks, or by blows upon the epigastrium; and this statement has been generally received upon his authority. It is far, however, from being constantly true; for Mr. Gulliver has made observations and collected numerous cases in which coagulation was found to have taken place in the blood of animals killed in each of these modes; in some of them, however, the coagulation was very imperfect.¶ It is not improbable that some of the instances of apparent *absence* of coagulation were really cases of *retarded* coagulation; and Dr. Polli goes so far as to maintain that the complete absence of coagulating power is a phenomenon which has no real existence. He states that he has never met with an instance in which the blood, when left to itself, and duly protected from external destructive influences, did not coagulate before becoming putrid; and that he has more than once found blood to coagulate, which had been taken in a fluid state from the vessels thirty-six or forty-eight hours after death.** Still there seems no reasonable doubt that non-coagulation *may* occur, when the blood has been previously subjected to conditions which affect its vitality. Such

* "Inquiry into the Nature and Properties of the Blood," 2nd ed. p. 66.

† "Proc. Roy. Soc.," 1858, xii. p. 580.

‡ Foster, "Physiology," 2nd ed. p. 22.

§ "Comment. de Sanguinis Coagulatione," Gröningen, 1820.

‖ "The Works of John Hunter," ed. James F. Palmer, vol. iii. pp. 34, 114.

¶ See "Edinb. Med. and Surg. Journ.," Oct. 1848, pp. 367, 418, and his Edition of "Hewson's Works," pp. 20, 21.

** "Annali Universali," 1845; and Ranking's "Abstract," vol. ii. p. 337.

appears to be the case, for example, when death occurs from Asphyxia, as by hanging, drowning, or breathing of irrespirable gases;* and the same has been observed in cases of poisoning by hydrocyanic acid, in which asphyxia was probably the immediate cause of death. In like manner certain animal poisons when introduced into the current of the circulation—as by the bite of venomous serpents—appear like a high temperature to entirely prevent the coagulation of the blood. In certain diseased states, again, the coagulating power seems to be completely deficient.

187. The rapidity of Coagulation, and the degree in which the clot solidifies, vary considerably; in general, they are in the inverse proportion to each other. Thus, if a large quantity of blood be withdrawn from the vessels of an animal at the same time, or within short intervals, the portions that last flow coagulate much more rapidly, as originally proved by Hewson, but much less firmly, than those first obtained. In blood drawn during Inflammatory states, again, the coagulation is usually slow, but the clot is preternaturally firm; especially at its upper part, where the Buffy coat (§ 181) or colourless stratum of fibrin gradually contracts, and produces the "cup," which may be generally considered to indicate a high degree of inflammation. The physical changes to which the blood is subjected when drawn from the vessels are, that it is brought to rest, that its temperature is reduced, and that it is exposed to the action of the air. It may easily be shown, however, that its coagulation cannot be attributed to either of these conditions. For, in the first place, if the blood be continually agitated in a bottle, though its coagulation is delayed, it will at last take place in shreds or insulated portions; yet that rest is not the cause of its coagulation (as some have supposed) is proved by the fact that, if a portion of blood be retained in the excised heart of a frog or turtle† by ligature of the vessels, or be included between two ligatures in a living vessel, it will, as mentioned above, remain fluid for a considerable time;‡ as it also will when effused into the midst of living tissues, or kept in a state of stagnation in parts affected with inflammation. Thus, Mr. Gulliver, besides other instances, mentions a remarkable case witnessed by himself, in which a collection of blood which had been effused in consequence of a bruise on the loins, was found uncoagulated when let out twenty-eight days afterwards; it measured five ounces, was as liquid as blood just drawn from a vein, and showed the normal characters when examined microscopically; and it coagulated in a cup in less than thirty minutes.§ And Sir James Paget mentions that he has known the blood remain fluid in the vessels of an inflamed part, though in a state of complete stagnation, for as long as three days.‖—Again, so far from coagulation being promoted by cold, it can be shown to be accelerated by moderate warmth, the natural heat of the body from which the blood is taken appearing to be most favourable to it; but the coagulating power appears to be destroyed by a temperature of about 150° F., blood heated to that point remaining permanently fluid.¶ On the other hand, the coagulation is retarded by cold; but the

* See Dr. J. Davy's "Physiological and Anatomical Researches," vol. ii. p. 191.

† "B. and F. Med.-Chir. Rev.," xix. p. 183, 1857.

‡ The testimony of all experimenters is in accordance on this point, although they differ as to the length of time that elapses before coagulation commences. Mr. Gulliver states that out of many trials made by him, the coagulation commenced within two hours in only a few instances; more commonly three, four, or five hours elapsed before any clot was formed; and in one instance the coagulation was incomplete at the end of twenty-four hours. In all these experiments, the blood coagulated in the course of a few minutes when withdrawn from the living vessels.—See Mr. Gulliver's edition of "Hewson's Works," p. 23.

§ Op. cit., p. 17.

‖ "Lectures on Surgical Pathology," vol. i. p. 310.

¶ Gulliver, op. cit., pp. 4, 5.

coagulating power is not destroyed even by extreme cold. Lastly, although coagulation is accelerated by exposure to air, it is not prevented by complete exclusion from it, as is proved by its taking place in a vacuum, or in a shut sac within the dead body; complete exclusion from the air, however, does retard the change, as may be easily shown by causing blood to flow into a vessel containing oil, which will form an impervious coating on its surface, and will occasion the coagulation to take place so slowly, that the red particles have time to subside, and the upper stratum of the clot to be colourless.*—The effect of the addition of strong solutions of neutral salts to fresh blood is usually to retard, and sometimes even to prevent, its coagulation; it is retarded also by pepsin,† and the same effect is produced by many vegetable substances, particularly those of the narcotic and sedative class, such as opium, belladonna, aconite, hyoscyamus, digitalis, and tea or coffee in strong infusion.‡ The action of most of these substances, however, which preserve the fluidity of the blood, only continues during such time as their solutions retain a certain strength; for if they be diluted coagulation will then take place, although in most cases less perfectly than it would have done at first. There appears to be no limit to the time during which the coagulation may be thus postponed; thus, Mr. Gulliver mentions that he has kept hare's blood fluid with nitre for fifty-seven weeks, and that it still readily coagulated when diluted with water.§ It is not so difficult therefore, as it might otherwise seem, to give credit to the statement of Dr. Polli,‖ that in a case witnessed by himself, complete coagulation of the blood did not take place until fifteen days after it had been withdrawn from the body, and that fifteen days more elapsed before putrefaction commenced in it. The upper four-fifths of the clot were colourless, the red corpuscles occupying the lowest fifth. It is additionally interesting to notice that the patient (who was suffering under acute pneumonia), being bled frequently during the succeeding week, the blood gradually lost its indisposition to coagulate, for as more blood was drawn, more white corpuscles would be found in it, and consequently more ferment would be liberated. Neither heat, ammonia, nor carbonic acid appear to be evolved, as was formerly supposed, during coagulation.

188. *Development of the blood corpuscles.*—The *first* Red corpuscles unquestionably have their origin, like the original cells of the solid tissues, in the primordial cells of the germinal structure; and it is in the 'mesoblast' or so-called 'vascular layer' of the 'blastodermic vesicle' (CHAP. XVIII. sect. 4), and the mass of cells which constitute the rudiment of the heart, that this metamorphosis seems first to take place. The situation of the heart, and the course of the principal trunks of the 'vascular area,' are early marked-out, by the peculiar disposition of the aggregations of cells from which these organs are to be developed; and whilst the *outer* portions of these aggregations are transformed into the *walls* of the respective cavities, the *inner* portions seem partly to deliquesce, and partly to remain as isolated cells floating in the liquid thus produced. These isolated cells are the first blood-corpuscles; and the following account of them in the Oviparous Vertebrata or Pyrenæmata is

* Dr. Babington in "Medico-Chirurgical Transactions," vol. xvi.

† Albertoni, "Centralblatt," 1878, p. 641.

‡ See Dr. J. Davy's "Anatomical and Physiological Researches," vol. ii. pp. 101, 102; and Mr. Prater's "Experimental Inquiries in Chemical Physiology," pp. 59, 63, &c. A copious table of the results of their experiments is given in Mr. Ancell's 'Lectures on the Physiology and Pathology of the Blood,' in the "Lancet" for Dec. 21, 1839.

§ Op. cit., p. 12.

‖ "Gaz. Med. di Milano," Genn. 20, 1844, cited in Mr. Paget's Report in "Brit. and For. Med. Rev.," xix. p. 252.

given by Foster and Balfour,* and differs but slightly from that by Klein:†—In the pellucid area, where the formation of blood-vessels may be most easily observed, a number of mesoblastic cells are seen to send out processes which unite and form a protoplasmic network, with nuclei at the points from which the processes started. The nuclei, which as a rule are much elongated and contain large oval nucleoli, increase very rapidly by division, and form groups at the nodal points. The majority of these acquire a red colour, and become converted into blood-corpuscles, but a few, generally on the outside of the group, remained unaltered. The protoplasm *in* which the central reddened nuclei are imbedded becomes liquefied, whilst that on the *outside* of each group as well that of the uniting processes remains granular and forms an investment for the unaltered nuclei which are imbedded in it. Each nodal point is thus transformed into a more or less rounded mass of blood-corpuscles floating in plasma, but enveloped by a layer of nucleated protoplasm, the several groups being united by strands of nucleated protoplasm. By the growth of the strands and the transformation of nuclei in their interior a series of communicating vessels is formed containing corpuscles which when removed from the vessels exhibit energetic amœboid movements, and probably increase by division.‡

189. That after the Chyle and Lymph have begun to flow into the circulating current, the *continued* generation of Red corpuscles is due to the progressive metamorphosis of those fluids, is an opinion which has come of late to be very generally received amongst Physiologists; it may be found, however, to require some modification. It rests upon the facts of three different orders:—1st, the presence, in the blood of oviparous Vertebrata, of corpuscles exhibiting what appear to be intermediate gradations of development between Lymph-corpuscles and the nucleated Red corpuscles, and this especially in blood in which an unusually rapid development of red corpuscles is taking place, to make up for previous loss; 2nd, frequent ruddiness in the hue of the fluid of the Thoracic duct, which seems to depend upon the incipient development of Hæmoglobin in some of its floating corpuscles; and, 3rd, the progressive transition from one form to the other, which may be observed in the ascending scale of animal existence. As to the precise mode, however, in which the non-nucleated Red corpuscles of Mammalian blood are produced, much difference of opinion still exists. The most probable view is that the ordinary

* "Elements of Embryology," 1874, p. 69.

† "Sitz.-ber. d. Wien. Akad.," 1871, Band lxiii. Abth. ii. For other accounts see Afanassieff, idem. Band liii. 1866, and Goette, Schultze's "Archiv," 1873; His, 'Neben die Erste Anlage des Wirbelthierleibs.'

‡ A different account has lately been given by Dr. H. D. Schmidt, *Monthly Microscopical Journal*, 1874, p. 45, from observations made on a very early human embryo. In this case the young coloured corpuscles appeared to be developed in the interior of mother-cells, at the expense of which they grew, and from which they ultimately became detached, leaving a dimple at the point of separation. One, two, or three young corpuscles were sometimes seen in a parent corpuscle, and the young ones themselves sometimes had a third generation in their interior prior to their own escape. This method of increase forms, as Dr. Schmidt observes, the transition from endogenous development to generation. The parent cells themselves appeared to be derived from the interior primary glandular follicles, formed of hexagonal cells in the walls of the umbilical vesicle, and he is of opinion that the so-called nuclei of the first set of blood-cells are in reality the embryonic red blood-corpuscles which, when first formed, exactly resemble the corpuscles of the adult, except that the central depression is less distinct. See also Schäfer, "Proceed. Roy. Soc.," xxii. No. 151, p. 243, who shows that blood-corpuscles arise in the interior of the vacuolated and nucleated cells of connective tissue; the hæmoglobin being deposited in the form of minute globules, which increase in size and form the corpuscles, whilst the cells elongating, branching, and uniting with others form the vessels.

lymph-corpuscle may either develop into a white corpuscle, or into a red corpuscle.* M. Hayem† gives the following account of certain cells, to which he has given the name of *Hæmatoblasts*, which he has found in the blood of the oviparous vertebrata, that is to say, in the Ichthyopsida, and Sauropsida :—These are destitute of colouring matter, yet differ essentially from the colourless corpuscles of the blood, and develop into perfect red corpuscles. The hæmatoblasts are at first very pale and delicate, of an angular and elongated form, with a solitary nucleus which is clearer than the body of the corpuscle, and which resembles the nucleus of the red blood-corpuscle, except that it is a little smaller and is less elongated. At this stage the hæmatoblasts differ from the white corpuscles, by the greater transparency and feebler refracting power of their protoplasm, and by their viscosity which causes them to adhere to one another, and so form masses of considerable size. As the development of the corpuscles proceeds the viscosity is lost, and the appearance of small discs is gradually assumed, whilst at the same time the hæmatoblasts become more darkly coloured, and the nucleus occasions a prominence on each side of the disc; at a still later period the protoplasm is reduced to a narrow ring round the nucleus, and the corpuscle assumes a shape resembling that of the developed red corpuscle. The colouring matter usually appears before the development of the cell is completed. All reagents act upon the hæmatoblasts just as they do upon the red blood-corpuscles, and produce none of the effects manifested by the leucocytes.‡ In no case are these hæmatoblasts less numerous than the white corpuscles, but, on the contrary, they may be twice as numerous. Mr. Wharton Jones still holds the view originally maintained by Hewson, that the red corpuscles of Mammalia proceed from the nuclei of the pale corpuscles; and it is almost certain that amongst the apyrenæmata the entire white corpuscle does not become the red corpuscle, though various observers have endeavoured to show that the pale nucleated cells of the pyrenæmata do pass into the coloured nucleated red corpuscle of this section of vertebrata. In that case the difference in the mode of development would appear as remarkable as the difference in the perfect structure, already described, of the red corpuscles of these two main divisions of Vertebrata. Under any circumstances the Chyle and Lymph seem to be continually supplying, not merely the *pabulum* for organization, derived from the food, whereby the components of the liquid part of the blood are replenished as fast as they are withdrawn; but also the rudimentary *corpuscles* which are to be progressively metamorphosed into the particles that float in its current. In one or two instances, under exceptional circumstances, the red blood-corpuscles have been seen to be undergoing fission.

190. *Composition of the Blood.*—The morphological or formed elements of the Blood having been thus separately described, we have now to inquire into the chemical characters of the various components which are associated in the liquid as a whole, and the proportions in which they severally present themselves. These are subject, even within the limits of health, to considerable variations; some of which seem to depend upon the constitution of the individual, his diet, mode of life, &c.; whilst others are probably referable to the period at which the last meal was taken, and the amount of bodily exertion made within a short time previous to the analysis. Taking the blood of the horse, Hoppe-Seyler found the following proportions:—

* See Dr. Bennett, "Lancet," vol. i. 1863, p. 378.
† Académie des Sciences. ‡ "Lancet," Dec. 29, 1877, p. 966.

In 100 parts of Blood.

Plasma, 67·38		Blood corpuscles, 32·62	
In 100 parts of Plasma		In 100 parts of Blood-corpuscles.	
Water	90·84	Water	56·50
Solids	9·16	Solids	43·50

Relative proportion of the Solids.		100 parts of dry Blood-corpuscles (Dog).	
Fibrin	1·01	Albumins	12·55
Serum albumin	7·76	Hæmoglobin	86·50
Fats	0·12	Lecithin	0·59
Extractives	0·40	Cholesterin	0·36
Soluble salts	0·64		
Insoluble salts	0·17		

191. We have now to notice those less prominent components of the Blood which have not been hitherto described in detail. Under the general head of *Fatty Matters* are included several different kinds of fat; of which the most important are the saponifiable fats, stearin, palmitin, and olein; the phosphorized fats or glycerin-phosphoric acids, which appear to originate from the decomposition of Lecithin (§ 56) in the blood, and cholesterin. The proportion of the saponifiable fats is always considerably increased after food, the increase proceeding from the entrance of the oleaginous chyle (§ 139). The kind of food will, however, of course materially affect the quantity of fat contained in the blood. Nasse found 2·6 parts of fat in 1000 of the blood of a dog that had been kept fasting for 4 days. After bread diet it rose to 3·1 parts, after meat to 3·8, and after suet and starch to 4·1 parts in 1000.—The following Table represents the mean, maximum, and minimum amounts of fatty substances in the healthy blood of Man (the proportion in that of the female being almost precisely similar), according to the analyses of MM. Becquerel and Rodier:—

	Mean.	Max.	Min.
Saponified fat	1·004	2·000	·700
Phosphorized fat	·488	1·000	·270
Cholesterin	·088	·175	·030
Serolin	·020	·080	inappreciable.

The source of the peculiar *odour* of the blood is probably a volatile fatty acid, too minute in its amount to admit of being separately estimated. This odour may be made much more apparent by treating the blood with sulphuric acid, even after it has been long dried; and in all those animals which are readily distinguishable by their odorous emanations, it may thus be made so perceptible as to admit of their blood being distinguished (at least by an individual possessed of a delicate sense of smell) through its scent alone. Of this test, use has been made with great advantage in juridical investigations.*

192. Under the vague term *Extractive*, have been included many different substances which normally present themselves in only very small quantity, and which are consequently difficult of detection, but which are extremely important in a physiological point of view, as the chief "factors" (to use the appropriate designation of Prof. Lehmann) in the metamorphosis of animal tissue, both *progressive* and *retrograde*. Amongst the latter, Urea, Kreatin, and Kreatinin; Uric, Hippuric, and Lactic Acids, Leucin, Tyrosin, and

* See M. Barruel's researches on this subject in "Ann. d'Hygiène," &c., tomes i., ii., and x.

Hypoxanthin (or Sarkin), may be particularly mentioned. Besides the foregoing, the extractive of blood generally seems to contain Sugar, or an amyloid substance, which is found most abundantly in the blood of the hepatic vein, vena cava, and pulmonary artery. As might be expected, the proportion of sugar in the blood is greatly affected by the diet of the animal. Plosz and Tiegel* have described a saccharifying ferment in the blood, and Hudson Ford† maintains that alcohol derived from the decomposition of sugar is normally present.—The very small amount in which the Blood-constituents of this class normally present themselves is readily accounted-for by the fact that they are only *en route* between the tissues and the excretory organs which are destined for their elimination; so that as long as the disintegrating processes taking place in the former are balanced (as they should be) by the activity of the latter, these substances are withdrawn from the blood-current as fast as they are introduced into it, and no sensible accumulation will occur. It can scarcely be doubted that the more attentive study of this part of the blood, prosecuted upon large quantities at once, will be attended with the discovery of many facts that would throw great light upon the Chemistry of the histogenetic operations, and of the retrograde metamorphoses of the effete materials of the tissues.

193. No list of the *Inorganic Constituents* of the Blood which has yet been given expresses the precise mode in which they are grouped together; for both the blood-corpuscles and the plasma contain phosphoric acid in combination with lecithin, and this acid, when the blood is incinerated, expels carbonic acid from its combinations, and if in excess of the carbonates also decomposes the chlorides, setting the chlorine free. So, again, in the incineration of albumins with sodium carbonate and free access of air, sulphates are formed by the oxidation of the sulphur in albumin. Schmidt found in 1000 parts by weight of blood of Man—

Potassium	1·739	Phosphoric acid	0·766
Sodium	1·902	Calcium phosphate	0·193
Chlorine	2·620	Magnesium phosphate	0·137
Sulphuric acid (SO_3)	0·094	Oxygen (estimated)	0·427

or about 8 parts in 1000. He has also attempted to give the distribution of the bases and salts in the corpuscles and plasma respectively, as is shown in the following Table—

In 1000 parts of Blood are contained

Plasma	487
Blood-corpuscles	513

1000 parts of Blood-corpuscles contain				1000 parts of Plasma contain			
Water, 681·63				Water, 901·51			
Solids, 318·37	Albumins	296·07		Solids, 98·49	Fibrin	8·06	
	Hæmatin	15·02			Albumins and Extractives	81·92	
	Salts	7·28	Potassium chloride 3·679 Potassium sulphate 0·332 Potassium phosphate 2·143 Sodium phosphate 0·633 Sodium 0·341 Calcium phosphate 0·094 Magnesium phosphate 0·060 Iron, undetermined		Salts	8·51	Common salt 5·546 Sodium 1·532 Sodium phosphate 0·271 Potassium chloride 0·359 Potassium sulphate 0·281 Calcium phosphate 0·298 Magnesium phosphate 0·218‡

* Pflüger's "Archiv," 1873, p. 391.

† "New York Med. Journal," vol. xv. 1872, p. 561.

‡ For fuller details the reader is referred to Hoppe-Seyler, "Physiol. Chemie," 1879, p. 451; and C. Schmidt, "Zur Characteristik d. Epidem. Cholera," Leipzig, 1850.

In Carnivorous animals the Phosphates, in Herbivorous the Carbonates, are in excess, which is obviously related to the difference of their diet. The normal presence of various metals in the blood has been alternately admitted and denied. Iron is unquestionably always present, and amounts to 0·42 per cent. of the hæmoglobin present.* Millon† found in 100 parts of the insoluble residue of the ash of blood 1 to 3 parts of silicon, 1 to 5 parts of lead, 0·5 to 2·5 parts of copper, and from 10 to 24 parts of manganese.‡ A trace of lithium has been discovered by means of the spectroscope (Folwarzny), and Küss admits a small proportion of arsenic.

194. We have now to inquire into the principal modifications which the relative proportions of these constituents undergo in the state of health, under the influence of varying conditions of the system; and notwithstanding the want of *absolute* correctness in the analyses of which we are at present in possession, those that are made by similar methods give results sufficiently trustworthy to enable them to be compared together, and thus to give a tolerably correct indication of the circumstances which determine the *increase* or *diminution* in the principal components of the blood.—The first of these modifying conditions which requires special notice is *Age*. During the latter part of fœtal life, the blood is remarkably rich in red blood-corpuscles and in iron, but contains less albumin, fat, and fibrin, than that of adults.§ The larger quantity of solid constituents in the blood of the fœtus appears to continue for a short time after birth; but it rapidly diminishes, and the whole amount of solid matter in the blood seems to fall to its lowest point during the period of childhood. Towards the epoch of puberty, the amount of solid matter increases again, the chief augmentation being in the corpuscles; and it remains at a high standard during the most vigorous period of adult life, after which it begins to decline. In old age it contains more water, fibrin factors, salts, and cholesterin, the number of corpuscles being less. This is made apparent in the following Table, deduced from the analyses of Denis, which are confirmed by those of Lecanu and Simon:‖—

						Solid Constituents.
In	5	individuals	between	5 months	and 10 years	170
	13	„	„	10 years	and 20 „	200
	11	„	„	20 „	30 „	240
	12	„	„	30 „	40 „	240
	6	„	„	40 „	50 „	240
	8	„	„	50 „	60 „	220
	9	„	„	60 „	70 „	210

The amount of oxygen in the blood also decreases towards the end of life.

195. An appreciable difference exists between the blood of the two *Sexes;* that of the male being from 12 to 20 per cent. richer in solid contents than that of the female, the excess being particularly observable in the proportion of the corpuscles. The blood of the woman is of less sp. gr. and of brighter colour. The serum contains less salts, though the total quantity of salts in the blood is

* See Fudakowski, "Centralblatt f. d. Medicin. Wiss.," 1866, p. 705.

† "Annal. de Chim. et de Phys." sér. iii. t. xxiii. p. 372.

‡ Melsens ("Annal. de Ch. et de Ph.," xxiii. p. 358) denies the presence of copper and lead and Béchamp ("Journ. de la Phys.," 1860, vol. iii. p. 211) appears to think the occurrence of all or any of these metals to be merely accidental.

§ Panum (Virchow's "Archiv," 1864, Band xxix. p. 481) found the blood of the new-born dog contained from 19·26 to 22·8 of solids, whilst that of the mother contained only 13·8 per cent. Leichtenstern ("Untersuch. üb. d. Hæmoglobingehalt des Blutes," Leipzig, 1878, p. 32) found the proportion of Hæmoglobin in the new-born dog as compared with the mother to be as 96 : 53.

‖ "Animal Chemistry," vol. i. pp. 237–239.

larger.* The corpuscles are fewer, but the albumin, fats, and extractives are present in larger proportions.† There is no doubt, also, that the proportions of the constituents vary considerably with individual *temperament* and *constitution;* the proportion of the whole solid constituents, and especially of the corpuscles, being considerably greater in individuals of the plethoric or 'sanguineous' temperament than in persons of the 'lymphatic' temperament; and it appears from the analyses of Lecanu,‡ that the sexual difference in the blood almost disappears when the blood of males and of females of the latter temperament is compared. There is no material change in the composition of the blood in the early months of pregnancy, but in the later stages the albumin and red corpuscles diminish, and there is an increase of fat, fibrin, water, and salts.§

196. A considerable influence is exercised on the entire amount, and on the relative proportions, of the constituents of the blood, by the previous ingestion of *Food or Drink*, and by the *Diet* habitually employed. When a full meal containing oily matter is taken after a long fast, and a small quantity of blood is drawn previously to the meal and at intervals subsequently, the serum, though quite limpid in the blood first drawn, shows an incipient turbidity about half an hour afterwards; this turbidity increases for about six hours subsequently, after which it usually begins to disappear. The period at which the discoloration is the greatest, however, and the length of time during which it continues, vary according to the kind and quality of the food, and the state of the digestive functions. When such milky serum is examined with the microscope, the opacity is found to be partly due to an increase in the amount of white corpuscles, and partly to the presence of an immense number of exceedingly minute granules, identical with those which form the 'molecular base' of the chyle (§ 155). They seem to be composed of two chemically distinct substances; for when the milky serum is agitated with ether, a part is dissolved, whilst another portion remains suspended; and this latter is soluble in caustic potash. The former, therefore, appears to be identical with the 'molecular base' of the chyle, and to be of an oily or fatty nature; whilst the latter belongs to the protein-compounds, and probably constitutes the haptogen membrane of Ascherson, by which all fatty particles floating in an albuminous fluid, immediately become invested. The Crassamentum of such blood often exhibits a pellucid fibrinous crust, sometimes interspersed with white dots; and this seems to consist of an imperfectly assimilated protein-compound, analogous to that found in the serum. The quantity of this varies according to the amount of the protein-compounds present in the food. The quantity of oxygen contained in arterial blood is diminished during digestion.—The increase of *saccharine* matter in the blood (in which it forms part of the 'extractive'), after the ingestion of a large quantity of saccharine or farinaceous aliment, has been noticed by many experimenters. Its proportion differs much in different parts of the body. It might be fairly presumed that a temporary augmentation must take place in the *aqueous* constituent of the blood, whenever any considerable quantity of liquid is ingested; and yet this augmentation is much less considerable, under ordinary circumstances, than we should at first be

* Beaunis's "Physiology," p. 105.

† In advanced pregnancy in the *dog*, Nasse ("Archiv f. Gynæcol.," Band x. 1877, p. 315) found that there was diminution in the sp. gr. of the blood with increase in the proportion of water, fat, fibrin, and salts. The blood only returned to its normal condition after lactation had ceased.

‡ "Etudes Chimiques sur le Sang humain," p. 66; and Simon's "Animal Chemistry," vol. i. p. 236.

§ See Nasse, "Archiv f. Gynæcol.," Band x. 1877, p. 315.

inclined to suppose. For there exist various provisions in the system (the peculiar Malpighian apparatus of the kidneys being the chief) for rapidly freeing the blood from any superfluity of water; and thus any excess of fluid absorbed is speedily drawn off again. But further, it is certain that when the vessels are already filled, absorption does not take place with nearly the same readiness as after long abstinence from liquids; the rate of absorption being in great degree governed by that at which the liquid is disposed of. The influence of the *Regimen* upon the composition of the blood, however, appears to be more definite and constant. An animal diet tends to increase the whole amount of solid matter, and particularly to augment the proportion of red corpuscles with hæmoglobin, extractives and salts, especially the phosphate and salts of potassium. On the other hand, a vegetable diet tends to lower the whole amount of solid matter, occasioning a marked reduction in the corpuscles, whilst it seems rather to increase the albumin, fats, sugars, calcareous and magnesian salts; thus showing that the decrease in the corpuscles is not due to a deficiency in the azotized pabulum, but depends on some other condition. The development of fibrin appears to take place at least as readily on the vegetable, as on the animal regimen. Hence we see what may, and what may not, be effected in the treatment of disease by the adoption of a particular dietetic system; for we may promote or retard the development of the red corpuscles by the employment of an animal or a vegetable regimen, but can make little or no impression upon the fibrin.*

197. The effects of *Loss of Blood* and of Abstinence are very similar in their nature. Almost as soon as the stream begins to flow from a wounded vessel, there seems to be a transudation of watery fluid from the tissues into the current of blood; for this undergoes a rapid diminution in density, so that the portion last drawn is of lower specific gravity, and contains a considerably smaller amount of solid matter than that which first issued. The principal diminution occurs in the proportion of red corpuscles; the amount of fibrin, albumin, extractive and saline matters and fat being only slightly affected.† We shall find, indeed, that in inflammatory diseases the amount of fibrin undergoes an extraordinary increase, which is not checked in the slightest appreciable degree by the most copious venesection. Considerable losses of blood are soon repaired, and it is remarkable that after very considerable losses of blood a decided increase shows itself in the proportion of Colourless corpuscles, not only *relatively* (as to the red) but *absolutely;* so that in the blood of a horse from which 50 lbs. have been previously abstracted, the coloured and the colourless corpuscles appear to exist in equal numbers.‡

198. *Pneumatology of the Blood.*—The Gases contained in the blood principally consist of Oxygen and Carbonic acid, the former being chiefly combined with the red corpuscles, the latter wholly with the saline constituents of the plasma. A small proportion of Nitrogen and traces of Ammonia are, however, constantly present. The absolute as well as the relative proportion of these gases differs, not only with the part of the system and the vessel from which the blood is drawn, but also with the globular richness of the blood,§ and to a remarkable extent with the mode of analysis adopted.‖ The mean amount

* See on this subject the treatise of M. Emile Marchand, "De l'Influence comparative du Régime Végétal et du Régime Animal sur le Physique et le Moral de l'Homme."

† See the Observations and Analyses of Zimmerman (Heller's "Archiv," Band iv. p. 385); Polli ("Med.-Chir. Review," Oct. 1847); J. Davy ("Anat. and Physiol. Researches," vol. ii. p. 28).

‡ Kölliker's "Manual of Human Histology" (Sydenham Society's edit.), vol. ii. p. 330.

§ See Mathieu and D'Urbain, "Archiv de Physiol.," 1871–72, p. 14.

‖ Thus the arterial blood of different dogs has been found by different observers to yield

of O in the arterial blood of a healthy dog is 22·2 vol. per cent., of CO_2 34·3 vol. per cent., and of N 1·8 vol. per cent., making a total of 58·3 vol. of gas in 100 vol. of blood. Venous blood in becoming arterial may absorb from 4 to 20 vol. per cent. of oxygen, and at the same time part with from 3 to 13 vol. per cent. of carbonic acid. Under ordinary circumstances it probably gains about 5 or 6 vol. per cent. of oxygen, and parts with about the same quantity of carbonic acid gas, the nitrogen remaining unchanged. There is perhaps a slight diminution in the quantity of O, and increase in the quantity of CO_2, as the blood passes from the larger vessels towards the capillaries, and about 1 per cent. of oxygen disappears from the blood in the course of the first minute after withdrawal from the body, its alkalinity simultaneously diminishing.* From the results of numerous recent researches, the conclusion may be drawn, that the affinity or capacity of absorption of the blood for both oxygen and carbonic acid gases at least, is peculiar, follows laws of its own, and differs materially from that of other liquids. In the case of Oxygen, if we compare it with water, we find that the coefficient of absorption of water for oxygen gas at 0° C. temp. and 760 mm. pressure is 0·04115. If the coefficient of absorption of blood for oxygen were the same, it would only absorb 0·86 vol. per cent. at 0° C., and still less of course at its ordinary temperature of 36° or 38° C., whereas it is known to be capable of absorbing at least 25·4 vol. per cent. at this temperature and at ordinary pressure. This remarkable power is due to the strong affinity for oxygen possessed by hæmoglobin, with which substance nearly the whole of the oxygen contained in the blood is combined to form oxyhæmoglobin. The hæmoglobin in arterial blood is almost saturated with O, whilst in venous blood a variable proportion of the oxyhæmoglobin exists in the reduced condition of hæmoglobin. If, as not unfrequently happens, 100 c.c. of blood contain 14 grammes of oxyhæmoglobin, 23·43 vols. per cent. of O can be extracted from it by means of the mercurial pump, or about 9-10ths of the amount required for its saturation,† and we may even, as Gréhant has shown, conversely regard the amount of oxygen capable of being extracted from blood as a measure of the quantity of hæmoglobin it contains—167·39 c.c. of oxygen at 0° C. and 760 mm. pressure representing 100 grammes of hæmoglobin.‡ The tension of the oxygen in arterial blood under normal conditions is equivalent to an O pressure of 78·7 mm. Hg, which is about one-half of the O partial pressure in the atmosphere at 0° C.§ The serum, as might be expected, contains very little oxygen; the gases of this fluid, according to Pflüger,‖ containing only 0·26 vol. per cent. O with 2·24 N and 35·26 vol. per cent. CO_2. The difference in the amount of oxygen absorbed by the blood in an animal exposed to high pressure from the normal amount is not very great. Thus, Paul Bert found that the blood of a dog contained, at ordinary pressure, 20·2 vol. per cent. of oxygen. When the animal was subjected to a pressure of five and a half atmospheres it was 23·7 vol. per cent., and under a pressure of ten atmospheres the amount had only increased to 24·7 vol. per cent. It would seem that there is a point of saturation of the hæmoglobin which is attained at low pressures, after which the blood

in some instances as small a quantity as 10·3 vol. per cent. of oxygen, and in others as much as 25·4 vol. per cent. The amount of carbonic acid has been found to be as low as 35 and as high as 45·6 vol. per cent., whilst the amount of nitrogen varies from 1·22 to 5·96 vol. per cent. In like manner the proportion of O in venous blood has been observed to vary from 5·5 to 16·5 vol. per cent., of CO_2 from 39 to 52 vol. per cent., and of nitrogen from 1·25 to 4 vol. per cent.

* Stroganow, Pflüger's "Archiv," Band xii. p. 48.

† Hoppe-Seyler, "Physiol. Chemie," 1879, p. 500.

‡ Hoppe-Seyler, "Physiol. Chemie.," 1879, p. 380. See also Solyet and Lafforet, "Jahresbericht für Physiologie," 1877, Band i. p. 134.

§ E. Herter, "Zeits. f. Phys. Chem.," Band. iii. 1879, p. 98.

‖ "Archiv f. d. ges. Phys.," Band i. p. 73.

only takes up more oxygen through the plasma, in accordance with the law of Dalton. The importance of the absorption of oxygen being dependent upon chemical affinity, and not simply upon pressure, is sufficiently obvious; since by securing the introduction of a definite proportion of this gas it enables animal life to be maintained without difficulty at all altitudes except the most extreme. Bert* found that when oxygen reaches the proportion of 28-30 vols. in 100 vols. of arterial blood in a dog the animal is seized with convulsions, while a proportion of 35 vols. proves fatal.

199. And so again with carbonic acid gas, whilst 100 vol. of water will absorb about 100 vol. at ordinary temperature and pressure, Meyer† found that 100 vol. of fresh defibrinated blood would take up 178·3 vol. of this gas at 48° F., the quantity increasing, though not in direct proportion, with the pressure. P. Bert, however, found that exposure of a living animal to an augmentation of pressure, even up to ten atmospheres, does not materially influence the amount of CO_2 contained in the blood; in fact, with high pressures, if the original proportion of CO_2 in the blood surpassed 38 vol. per cent., the amount actually diminished, a circumstance that does not admit of ready explanation. The tension of the CO_2 in ordinary air amounts to 0·38 mm., corresponding to 0·05 per cent. by volume; but in arterial blood it amounts on an average to 21 mm.—*i.e.*, to the tension of the gas in an atmosphere containing 2·8 per cent.; and in venous blood to 41 mm., or to the tension of the gas in an atmosphere containing 5·4 per cent.‡ It is very evident, then, that the absorption of this gas also does not take place in accordance with the ordinary law established by Dalton and Henry, but that chemical affinity must come into play; and the general results of recent inquiry shows both the blood-corpuscles and the plasma or serum contain CO_2 in such loose combination that it is given off, in part at least, in the vacuum of a mercurial pump; the serum retaining it more strongly than the red blood-corpuscles. The addition of an acid causes the elimination of a further quantity. Thus Pflüger, from a very pure specimen of serum, obtained 35·2 vol. per cent. of CO_2 on exposure to a vacuum, and an additional 9·3 vol. per cent. on admixture of phosphoric acid. The red corpuscles are capable of acting like an acid upon the serum, and effecting the expulsion of its CO_2, and the action is more energetic in proportion to the amount of oxyhæmoglobin they contain. Even the albumins of the serum appear to possess a similar power, and to act like an acid in expelling CO_2 *in vacuo*. It has been suggested that the CO_2 is in combination in the serum with the carbonate and phosphate of soda,§ since dilute solutions of these salts in water increase its absorption power for CO_2; in the former case a bicarbonate, and in the latter a peculiar double salt $PO_3 + Na_2 + CO_2$, being formed; but Sertoli‖ has shown that the amount of the phosphates in the blood is insufficient. As regards Nitrogen, the coefficient of absorption of water for it at 0° C. and 760 mm. pressure is 0·020316, and 100 vol. of water would therefore absorb 1·608 vol. of N.; and blood seems to follow this law, the average proportion being 1·8. The amount which the blood contains in the living animal is essentially dependent

* "Comptes Rendus," No. 8, Aug. 25, 1873.

† "Zeitschrift f. Rat. Med.," Band viii. p. 256.

‡ See Hermann, op. cit., p. 140, quoted from Strassburg. Wolffberg, Pflüger's "Archiv," Band iv. Heft x., found that the tension of the O in the blood of the pulmonary capillaries amounted to 27 mm. of mercury, and that of the CO_2 to 24 mm.

§ "La pression barometrique," 1878, p. 669.

‖ See Heidenhain's "Studien des Physiol. Instit. zu Breslau," 1863, p. 103; Pflüger, "Centralblatt für die Med. Wiss.," 1867, Nos. 21 and 46.

on the pressure to which the animal is exposed, though it does not precisely follow the law of Dalton, a smaller quantity being absorbed under increased pressure than that law requires. Thus, Paul Bert* found that exposure to 10 atmospheres augmented the amount of N from 2·2 vol. per cent., which was about the normal proportion, to 11·3 vol. per cent. only, whilst if Dalton's law had been followed 22 vol. per cent. should have been absorbed.

200. Besides the differences above described in the proportion of the gases contained in arterial and venous blood, there are several other points which are deserving of notice. Thus, the temperature of arterial blood is usually regarded as a trifle lower in temperature than venous. Its colour is brighter and monochroic, it coagulates rapidly; the number of corpuscles and the quantity of water, fibrin and salts is greater, whilst that of fat is less. Venous blood, on the other hand, is warmer, darker red, dichroic, coagulates more slowly; the number of corpuscles and the quantity of fat is greater, and that of water, fibrin and salts less. The experiments of Dr. Gairdner† seem to show that increase in the relative proportion of oxygen in the blood increases the proportion of fibrin that may be obtained from it, thus the arterial blood of six healthy rabbits furnished the following mean per-centage results:—Fibrin 1·65, Corpuscles 82·35, Albumin 46·30. On the other hand, the analysis of the blood of three individuals which had been made to respire pure oxygen for half an hour, gave the following as the proportions of its components:—Fibrin 2·40, Corpuscles 69·56, Albumin 40·23. It is further stated by Dr. Gairdner,‡ that a rabbit having been kept for half an hour under the influence of an electro-magnetic current between the chest and spine, which produced a great acceleration in the respiratory movements, its blood was found to contain as much as 2·9 parts of fibrin in 1000.§—The larger quantity of fibrin in arterial blood of itself renders its coagulum firmer; but independently of this there would seem to be a difference in the quality of the fibrin, which when separated by stirring or whipping, is more tenacious and compact in arterial than in venous blood. The varying circumstances under which either arterial or venous blood may be at one time dark and at another scarlet in colour, were very fully discussed by Wells‖ and Bernard.¶ The latter observes that in the Fœtus, and in the asphyxiated animal, the blood is everywhere dark or venous. On the contrary, during sleep, in the hibernants during the period of repose, and in animals dying by anæmia, the blood is everywhere scarlet or arterial. With high temperatures of the surrounding medium, whether this be air or water, there is little difference in the colour of the two kinds of blood, the arterial being less and the venous more florid than usual.** The difference between them is, on the other hand, best marked in cold weather. The Blood contained in the veins of muscles is dark, and always of a deeper shade in proportion to the energy and duration of the previous muscular contraction, whilst that returning from the glands is always brighter in proportion to the activity with which secretion is being performed; and in the latter instance, with the alteration in colour, the amount of fibrin is found to

* "Centralblatt f. d. Med. Wiss.," 1868, No. 10.

† "Treatise on Gout," 2nd edit. p. 153. ‡ Op. cit., p. 183.

§ Mr. A. H. Smee ("Proceedings of the Royal Society," 1863) and v. Gorup-Besanez ("Physiolog. Chemie," 1862, p 137) have stated that they have obtained a fibrin-like substance; the former, by transmitting Oxygen, and the latter Ozone, through an albuminous fluid, but it was probably some modification of albumin.

‖ "Phil. Trans.," 1797. ¶ "Leçons," xi. to xix. 1859.

** See an account of Davy's and Crawford's Experiments in Gulliver's Lectures, "Med. Times and Gaz.," 1863, vol. i. p. 1.

be diminished, or so modified as to form a softer clot, from which a larger quantity of serum separates. The variations which occur in the gases of venous blood returning from muscles at rest and in action, as compared with the arterial blood of the same animal, are well shown in the following results obtained by Sczelkow,* where A indicates Arterial blood, MR the blood returning from muscles at rest, and MA that returning from muscles in action:—

Total Gas.		O	N	Free CO_2	Combined CO_2	Total CO_2
A	43·515	17·334	1·636	24·204	0·341	34·545
MR	40·450	7·5	1·364	31·036	0·550	31·586
MA	37·069	1·265	0·923	34·443	0·438	34·881

In other experiments Sczelkow found that the venous blood returning from muscles at rest contained on the average 6·71 per cent. more carbonic acid and 9 per cent. less oxygen than arterial blood, whilst that returning from muscles in action contained an excess of 10·79 per cent. of carbonic acid, and a deficit of from 12 to 14 or even 16 per cent. of oxygen; and similar results were obtained by Bernard.† It is remarkable that if the dark-coloured clot of ordinary venous blood be immersed in the serum of the scarlet venous blood, it rapidly assumes a brighter tint, and conversely the clot of scarlet venous blood changes to a dark colour when immersed in the serum of deeply-coloured venous blood; from which we may conclude that the primary changes are effected upon the Liquor Sanguinis, and not upon the corpuscles. The influence of the Nervous System in inducing alterations in the colour of the blood returning from the salivary glands has already been pointed out (§ 106).

201. Although but little difference except as regards the relative proportion of oxygen and carbonic acid gases present can be detected between samples of blood drawn from various parts of the *Arterial* system of the same animal, very important variations exist, as might be expected, in the composition of the blood drawn from the several parts of the *Venous* system; since the changes to which it has been subjected in the several organs through which it has passed, are of a very diversified character. The blood of the Vena Portæ, for example, differs considerably from the blood of the Hepatic vein, and both of these differ from the blood of the Jugular. So, again, the blood of the Splenic as well as that of the Renal vein differs from all the preceding. The most important and best-established of these diversities will now be enumerated. The best as well as the most recent comparison between the blood of the vena portæ and that of the vena hepatica has been made by Drosdoff,‡ under Hoppe-Seyler's direction. The animals employed were dogs which were fed with meat, bread, and milk three or four hours before the blood was withdrawn. No attempt was made to estimate the amount of fibrin, and the coagulation of the blood was not awaited, but it was immediately whipped, and watery, ethereal and alcoholic extracts made of the remainder. Constant differences were observed, of which some only admit of explanation on the supposition that they are the result of changes taking place in the liver, whilst the cause of others is more doubtful. In four carefully-conducted

* "Sitzungsbericht d. Wiener Akad.," Band xlv. 1862.

† "Leçons," vol. ii. 1859, p. 435.

‡ "Zeits. f. Phys. Chemie," 1878, p. 233.

analyses the blood of the vena portæ was invariably richer in solid constituents than that of the hepatic vein, the difference in this and other respects being shown in the following Table :—

	Portal Vein.	Hepatic Vein.
Water	725·8	743·3
Solids	274·2	256·6
Hæmoglobin, albumins, and insoluble salts...	251·7	237·8
Cholesterin	2·6	2·7
Lecithin	2·4	2·9
Fats	5·7	0·9
Alcoholic extractives	1·2	1·3
Water extractives	5·0	5·6

The excess of fats in the portal vein is remarkable. In speaking of the composition of the blood of the *Vena Portæ*, it must be remembered that this consists of two very distinct factors—namely, the blood of the Gastric and Mesenteric veins, and the blood of the Splenic vein; the former having been altered by the introduction of solid and liquid alimentary matters, and the latter by its circulation through the spleen. These, therefore, ought to be separately studied; and this has been done by M. Jules Béclard.* The characters of the blood returning by the *Gastric* and *Mesenteric* veins from the walls of the alimentary canal are, of course, affected by the stage of the digestive process, and by the nature and amount of the absorbable matters. As compared with the ordinary venous blood, the total quantity of its solid constituents is lowered during the early part of the digestive process, by the dilution it suffers through the imbibition of liquid; and this diminution is especially remarkable in the corpuscles, the relative proportion of albumin being increased by the introduction of new albuminous matter from the food. Towards the conclusion of the digestive process, however, the blood of the mesenteric veins gradually comes to present the ordinary proportions of these two components; and in an animal that has been subjected to long abstinence, it does not differ from that of the venous system in general. The quantity of extractive is usually increased; and in this part of the blood it must be, that sugar, dextrin, gelatin, and other soluble organic matters that are taken into circulation are contained. Some of these have in fact been detected in it.† The fibrin of the blood of the mesenteric veins appears to be less perfectly elaborated than that of the blood in general; for the blood of the mesenteric veins coagulates less firmly (having been erroneously asserted by some not to coagulate at all); and its fibrin, when separated by stirring, shows a marked deficiency in tenacity, and liquefies completely in the course of a few hours. A part of the albuminous constituent of this blood does not present the characters of true albumin, for it is not precipitated by heat or by nitric acid, and the precipitate thrown down by alcohol is redissolved by water; like albumin, however, it is precipitated by the metallic salts, creasote, and tannin. This substance, which has been distinguished by M. Mialhe as *albuminose*, is in fact a peptone, differing from true albumin in the facility with which it traverses organic membranes; for these resist the passage of albumin, while they are freely transuded by peptone. And it is affirmed by M. Mialhe that the want of that conversion of albuminose into albumin, which ought to take place as part of the assimilating process, is one cause of the readiness with which albuminous matter transudes from the blood in albuminuria and

* See his Memoir in the "Arch. Gén. de Méd.," 4e série, tom. xviii. p. 322, *et seq.*; and his edition of his father's "Elémens d'Anatomie Générale," pp. 265, 266.

† See the Researches of MM. Bouchardat and Sandras in the "Supplément à l'Annuaire de Thérapeutique," 1846.

in dropsies; this albuminous matter frequently having rather the characters of albuminose, than those of true albumin.*

202. The Splenic blood is remarkable for the marked decrease it presents in the amount of solid matter it contains; the average of twelve experiments giving only 187·1 per 1000 of solid constituents in the splenic blood, whilst the arterial blood of the same animals contained 239 parts, and the jugular venous blood 201 parts.† The decrease depends upon the diminished proportion of *red* corpuscles. The albumin and fibrin, on the other hand, with the white corpuscles, are usually more or less increased in their relative proportions, the fibrin having been found in amounts varying from 2·5 to 11·53 parts in 1000, and coagulation having been noticed to recur when the blood had already been freed from the fibrin by whipping. Hirt‡ counted 1 colourless to 2179 coloured corpuscles in the blood of the splenic artery, but 1 colourless to 60 coloured in that of the splenic vein. The red corpuscles sometimes present crystals in their interior. M. Malassez§ remarks that the corpuscles are *really* more abundant in the blood of the splenic vein, and fewer in that of the hepatic vein, because they are formed in the spleen and destroyed in the liver. They are *apparently* diminished in the mesenteric veins during digestion, owing to absorption of fluid; and apparently increased in the blood of the skin, glands and tissues generally, owing to the exosmose of the fluid parts. It cannot be doubted that when the secretion of urine is proceeding with rapidity, the blood of the *Renal vein* must contain a smaller proportion of water than that of the renal artery, and that the quantity of salts also must be diminished; since a separation of these ingredients takes place in the passage of the blood through the renal capillaries. So far as regards the quantity of water this *à priori* conclusion has been confirmed by the analysis of Simon, who found 790 parts of water in 1000 of blood drawn from the renal artery, and only 778 in blood drawn from the renal vein of the same animal.‖ And Picard¶ found in the renal arterial blood of two dogs 0·0365 and 0·04 per cent. of Urea, whilst in the venous blood returning from the kidneys the proportion was 0·0186 and 0·02 per cent. Poisseuille and Gobley,** however, did not find the difference so well-marked or constant.

203. *Alterations in the Composition of the Blood in Disease.*—Under this head it is intended here to consider, not the state of the Blood in every principal type of disease (which it is the duty of the Pathologist to investigate), but the most important facts which the study of its morbid conditions has afforded, towards the determination of the conditions under which decided variations take place in the quantity or quality of its principal components, and of the effects which those variations produce upon the system at large. Many analyses have been made by excellent observers;†† but in consequence of the variations in the mode of analysis pursued, the results can only be given in general terms.

204. The first of these components whose variations we shall consider, is *Fibrin*: the estimate of which, however, is open to an important fallacy, that

* See the "Cours de Physiologie" of M. Paul Bérard, tom. iii. p. 87.

† See the Analyses of Mr. Gray in his Essay "On the Structure and Uses of the Spleen," 1854.

‡ Müller's "Archiv," 1856.

§ "Lond. Med. Record," 1874, p. 132.

‖ Simon's "Animal Chemistry" (Sydenham Society's ed.), vol. i. p. 214.

¶ Picard, "Sur la Présence de l'Urée dans le Sang," Strasbourg, 1856.

** "Comptes Rendus," 1859, p. 164.

†† See Andral and Gavarret, "Essai d'Hæmatologie Pathologique;" Becquerel and Rodier, "Recherches sur la Composition du Sang," &c.

has not been sufficiently guarded against—namely, the admixture of the Colourless corpuscles. "These," as Sir James Paget correctly remarks, "cannot, by any mode of analysis yet invented, be separated from the fibrin of mammalian blood; their composition is unknown, but their weight is always included in the estimate of the fibrin. In health they may, perhaps, add too little to its weight to merit consideration; but in many diseases, especially in inflammatory and other blood-diseases in which the fibrin is said to be increased, these corpuscles become so numerous that a large proportion of the supposed increase of the fibrin must be due to their being weighed with it. On this account all the statements respecting the increase of fibrin in certain diseases need revision."* In the results of the analyses now to be stated, it must be borne in mind that the term 'fibrin' really designates the 'colourless coagulum' of spontaneous formation, whatever may be its composition. The following may be considered as the normal range of variation for the principal constituents of the blood in health, according to the mode of estimating them pursued by MM. Andral and Gavarret:—

Fibrin	from	2	to	3½	parts per 1000
Red corpuscles . .	„	110	„	152	„ „
Solids of serum . .	„	72	„	88	„ „
Water	„	760	„	815	„ „

205. The most important fact substantiated by Andral, is one that had been previously suspected,—the invariable increase in the quantity of Fibrin during acute Inflammatory affections, as pleurisy and pneumonia, the increase being strictly proportional to the intensity of the inflammation, and to the degree of symptomatic fever accompanying it. "The augmentation of the quantity of Fibrin is so certain a sign of Inflammation, that, if we find more than 5 parts of fibrin in 1000, in the course of any disease, we may positively affirm that some local inflammation exists." The average proportion of Fibrin in inflammation may be estimated at 7; the minimum at 5; the maximum at 13·3. The greatest augmentation is seen in Pneumonia and Acute Rheumatism. Such blood in general coagulates slowly.† An increase is also commonly observable during the advanced state of Phthisis, in spite of the deterioration which the blood must then have undergone, and this is probably dependent upon the development of local inflammation around the tubercular deposits. In Continued and Typhoid Fevers, whilst the proportion of Corpuscles is commonly increased, there is a decrease in the proportion of Fibrin, especially in the early stage; though the usual augmentation will take place if any local inflammation occurs. It appears from the experiments of Magendie, that one of the effects of a diminution in the proportion of Fibrin is a tendency to the occurrence of Hæmorrhage or of Congestion, either in the parenchymatous tissue or on the surface of membranes; and these conditions are well known to constitute common complications, not only of febrile diseases, but also of Apoplexy and Purpura hæmorrhagica, in both of which there is a marked deficiency of Fibrin. It has been asserted that the proportion of Fibrin is diminished in Scurvy; but this, from the analyses of MM. Becquerel and Rodier, Chatin and Bouvier,‡ and Mr. G. Busk,§ appears not

* Morrant Baker's "Handbook of Physiology."

† The white fibrinous clots found after death in the heart and large arteries in various diseases appear to owe their origin to the slight disposition of the blood in these cases to coagulate, thus affording time for the sinking or separation of the red corpuscles. Mayer has augmented the amount of fibrin in the blood of dogs to nearly double its normal amount by repeated bleedings, repeated at stated intervals (quoted in Brücke's "Vorlesungen," 1874, p. 117).

‡ "Journ. de Chemie Médicale," Mars, 1848.

§ "Library of Medicine," vol. v. p. 90. See also Chalvet, "Union Médicale," 1871, p. 525.

to be the case, the proportion of fibrin being rather above than below the normal average. In Cholera, however, a reduction in the coagulable element of the blood seems to be an almost constant occurrence; and in some instances, the blood, although loaded with solid matter, has scarcely coagulated at all. Of the blood drawn during life, it has been observed that the clot is loose and grumous, often not shrinking and expelling serum; and that this change presents itself in a degree corresponding to the severity and advanced stage of the disease. And when the blood has been removed from the body after death, the clots have been found loose and fragile in texture, sometimes almost semi-fluid.* How far the so-called exudation found in an inflamed part is dependent upon the accumulation of the white corpuscles on the exterior of the vessels, as described by Waller and Cohnheim, cannot as yet be stated with certainty.

206. The amount of *Red Corpuscles* seems to be subject to great variation within the limits of ordinary health. It may even form a racial characteristic, for Mr. Bakewell† states that he was able to distinguish the Mahommedan from the Hindoo by the proportion of corpuscles contained in their blood, and both of these races readily from the negro, the blood in the latter race being very highly corpusculated. In the condition which is ordinarily termed a highly sanguineous temperament, or Plethora, it is chiefly the entire mass of the blood that undergoes an increase; but whatever excess there may be in the proportion of its solid constituents, this affects the corpuscles rather than the fibrin, the proportion of these, according to Mantegazza,‡ rising from 5,000,000, which is the normal amount, to 5,500,000, in a cubic millimetre. Plethoric persons are not more prone to inflammation than are those of weaker constitution; but they are liable to congestion, especially of the brain, and to apoplexy or other hæmorrhage. The effect of bleeding in diminishing this tendency is now intelligible, since we know that loss of blood reduces the proportion of corpuscles. On the other hand, in that temperament§ which, when exaggerated, becomes anæmia, there is a marked diminution of the corpuscles, the number contained in a cubic millimetre falling from 5,000,000, which is the normal amount, to about 2,000,000. This temperament may lead, on the one hand, to chlorosis, in which the proportion of red corpuscles, and especially of their hæmoglobin contents,‖ are diminished, a condition of the system which is singularly improved by the remedial employment of Iron;¶ and, on the

* See Dr. Parkes' "Researches into the Pathology and Treatment of the Asiatic or Algide Cholera," pp. 32, 73.

† "Med. Times and Gazette," Nov. 1872, p. 514. Also a Paper read before the Anthropological Society.

‡ "Gaz. Med. Ital." 1865, Nos. 23 and 25.

§ The term *lymphatic* has been applied to this temperament; by which term was meant a predominance of lymph in the absorbent vessels.

‖ See Hayem, "Recherches sur l'Anat. Norm. et Path. du Sang," Paris, 1878; Leichtenstein "Untersuch. üb. die Hæmoglobingehalt d. Blutes," Leipzig, Vogel, 1878.

¶ The records of Medicine scarcely furnish a more notable example of the pernicious influence of theories founded upon a shallow Empiricism, and of the superiority of a Rational practice, based on a knowledge of the real facts of the case, than is afforded by the contrast between the former and the present treatment of *Chlorosis*. Whilst the notion prevailed that the 'buffy coat' is a sign of Inflammation, and that the most potent remedy for Inflammation is loss of blood, patients already reduced to a state of anæmia, who complained of pain in the left hypochondrium, palpitations, &c., were bled over and over again, every withdrawal of blood of course seriously increasing the mischief, by producing a further reduction in the proportion of red corpuscles. The Author well remembers that, when a pupil in the Bristol Infirmary in the years 1833–34, he was repeatedly directed by the estimable Senior Physician (long since dead) to draw eight, ten, or twelve ounces of blood from patients in this condition; and that the crassamentum, after coagulation, often resembled a small island floating in an ocean of serum. Yet, because this minute clot exhibited the buffy coat, the bleeding was considered to be 'orthodox' practice, and the obstinacy of the symptoms

other, to Scrofula, in which a diminution of Corpuscles coexists with a deficiency in the amount or in the degree of elaboration of the Fibrin. A similar deficiency in the proportion of red corpuscles has been observed by Andral in other cachectic states induced by disease, as in Diabetes Mellitus, Aneurismal Dilatation of the Heart producing Dropsy, and in Cachexia Saturnina. It occurs also in Scurvy, and in the advanced stages of Albuminuria; and Dr. Williams* has observed extraordinary destruction of the blood-discs in a case of malignant scarlatina with purpura; and has met with indications of a partial destruction of them in acute purpura connected with jaundice, and in cases of functional derangement of the liver.

207. A marked increase in the proportion of the *Colourless Corpuscles* has been frequently observed in the blood of Inflammatory subjects; this increase is not, however, so characteristic of the Inflammatory state as some have supposed; for it is by no means constant in that condition, and is frequently seen in very different states of the system.†—Attention has recently been drawn by Prof. J. H. Bennett‡ to a condition of the blood which is especially characterized by a marked excess of these bodies, and which he has designated by the term *Leucocythæmia* (white-cell blood). This condition has been detected in the blood of a considerable number of individuals suffering under diseases (most commonly, enlargement) of the Spleen, Liver, and Lymphatic Glands, either separately or in conjunction; but it has not yet been determined how far it is constantly associated with any of these abnormal conditions. In all cases in which such blood has been analyzed, its specific gravity has been found very low, and the total amount of corpuscles small; but the fibrin is almost invariably above the average, having in one instance risen to 7·08.

208. The quantity of *Albumin* in the blood seems to vary less than that of most of its other constituents. The proportion which it bears to the water of the serum is, of course, elevated by anything which diminishes the latter; and thus we find it high in cholera after profuse discharges of fluid from the intestinal canal, and in other cases in which there has been an unusual drain upon the liquid part of the blood, provided that the albumin do not pass off with it, as sometimes happens. Where some special cause is in operation, which favours the escape of the albumin from the circulating current (as happens in various forms of albuminuria, but especially in the advanced stage of 'Bright's disease'), the amount of albumin in the serum is reduced below the normal standard. Thus, Dr. Christison found the entire solids of the serum to be reduced in some instances to 55 or even 52 parts in 1000, his estimate of their normal amount being 83·4; and he found the specific gravity of the serum to fall as low as 1020 or even 1019, the normal standard being from 1027 to 1031. According to Andral, the diminution in the amount of albumin in the serum is exactly proportional to the quantity contained in the urine.§ The propor-

was attributed to the severity of the disease. If M. Andral had made no other contribution to Medical Science than the demonstration of the real nature of this condition of the blood, and of the influence of further depletion in promoting it, he would have rendered a most essential service to the multitude of females who are unfortunate enough to suffer from this kind of deterioration of their vital fluid.

* "Principles of Medicine," 2nd edit. p. 115.

† As in Scurvy. See Laboulbène, "La Revue Scient.," sér. ii. an. 1, p. 43, 1871.

‡ See his successive Papers in the "Edinb. Monthly Journal" for 1851, his Treatise "On Leucocythæmia," and his Clin. Lectures "On the Principles and Practice of Med.," 4th edit. 1865, p. 867, *et seq.*

§ A case is related by Andral, under this head, which affords an interesting exemplification of the general facts that have been attained by his investigations. A woman who had been suffering from Erysipelas of the face, and had lost blood both by venesection and by leeches, became the subject of Albuminuria. The blood drawn at this time exhibited a considerable

tion of albumin is not diminished in scurvy (Chalvet). The proportion of *fatty* matter in the serum, and especially of the cholesterin, has been found by MM. Becquerel and Rodier to undergo an increase at the commencement of most acute diseases; and they have also observed an increase of fat, and especially of cholesterin, in chronic diseases of the liver, in Bright's disease of the kidney, and in tuberculosis. The quantity of fat in the blood sometimes undergoes such an augmentation as to give to the serum a constant 'milkiness.' This has been observed by Marcet in a case of diabetes, by Traill in hepatitis, by Christison in dropsy, icterus, and nephritis, by Zanarelli in pneumonia, and by Sion in mammary abscess. In Dr. Sion's case, the blood itself was quite milky; it underwent no coagulation; and only a very small quantity of colouring matter was deposited, when it was allowed to stand. This blood was found by Lecanu to contain 206 parts of solid constituents in 1000; but of these no less than 117 parts were fat, the remainder consisting of albumin (64 parts), and of extractive and salts (25 parts).* No fibrin could be found, and the quantity of hæmoglobin was inappreciable.† Such a fluid must be considered rather as chyle than as blood; and in the entire absence of coagulating power, corresponds rather with chyle when first absorbed, than with that which is usually transmitted by the thoracic duct.—Little is known with certainty regarding the variations of the *alkaline salts* in the blood in different diseases. The analyses which have been made, however, are considered by Prof. Lehmann‡ to indicate that in very severe inflammations they are greatly diminished; whilst they are much increased in the acute exanthemata and in typhus, in dysentery, Bright's disease, and all forms of dropsy and hydræmia; and are often doubled in quantity in diseases depending upon malarious influences, such as endemic dysentery, malignant forms of intermittent fever, &c. Although a large quantity of saline matter usually passes off from the blood in cholera, yet the proportion of water discharged is so much greater, that, as appears from the analysis of Dr. Garrod, the per-centage of salts in the blood is rather increased than diminished.§ The proportion of *water* in the blood will, of course, vary reciprocally with that of the solid constituents; and will be specially augmented when there is a marked diminution in the amount of red corpuscles.

209. That the Blood is subject to a great variety of other morbid alterations,

diminution in the proportion of the Red Corpuscles, as well as of Albumin,—a fact which the previous loss of blood fully accounted for. After a short period, during which she had been allowed a fuller diet, another experimental bleeding exhibited an increase in the proportion of those Corpuscles. Some time afterwards, when the Albumin had disappeared from the Urine, some more blood was drawn; and it was then observed that the Albumin of the Serum had returned to its due proportion, but that the Corpuscles had again diminished, whilst there was a marked increase in the quantity of Fibrin. This alteration was fully accounted for by the fact that, in the interval, several lymphatic ganglia in the neck had been inflamed and had suppurated; and that the patient had been again placed on very low diet. "Thus," observes Andral, "we were enabled to give a complete explanation of the remarkable oscillations which were presented in the proportion of the different elements of the blood, drawn at three different times from the same individual; and thus it is that the more extended are our inquiries, the more easy does it become to refer to general principles the causes of all those changes in the composition of the blood, which, from the frequency and rapidity with which they occur, seem at first sight to baffle all rules, and to take place, as it were, at random. In the midst of this apparent disorder there is but the fulfilment of *laws;* and, in order to obtain these, it is only necessary to strip the phenomena of their complications, and reduce them to their simplest form."

* See also a case by Speck, "Archiv f. wiss. Heilk.," 1864, p. 232.

† This remarkable case is cited in Simon's "Animal Chemistry," vol. i. p. 333, from the "Lancette Française," 1835, No. 49.

‡ "Physiological Chemistry" (Cavendish Society's ed.), vol. ii. p. 262.

§ "London Journal of Medicine," May, 1849.

which are sometimes the causes, and sometimes the results of Disease, cannot be for a moment doubted. But our knowledge of the nature of these changes is as yet very insufficient.* The great amount of attention which is being directed by Chemists and Pathologists to the subject, however, will doubtless ere long produce some important results.—Among the most frequent causes of depravation in the character of this fluid, we must undoubtedly rank the retention, in the Circulating current, of matters which ought to be removed by the Excretory processes. We shall hereafter see that a total interruption to the excretion of Carbonic Acid by the lungs will occasion death in the course of a very few minutes; and even when only a slight impediment is offered to the elimination of the carbonic acid, so that the quantity of it always contained in arterial blood is augmented to but a small degree, a feeling of discomfort and oppression, increasing with the duration of the interruption, is speedily produced. The results of the retention of the materials of the Biliary and Urinary excretions will be hereafter considered (CHAP. XI.); and at present it will be only remarked that such retention is a most fertile source of slight disorders of the system, that it is largely concerned in producing many severe diseases, and that, if complete, it will most certainly and rapidly bring about a fatal result.

3. *Of the Vital Properties of the Blood, and its relations to the Living Organism.*

210. It cannot be doubted that the perfect and regular performance of the various actions to which the Blood is subservient is dependent upon the admixture of its principal components in their due proportions, and upon its freedom from deleterious matters whether formed within the system, or introduced into the circulating current from without. And it is not difficult to

* It seems not improbable that the phenomena of disease are sometimes caused by, though perhaps in other instances they may be only associated with, the development of living organisms in the blood. Thus extremely fine, moving thread-like bodies resembling spirillum, have been observed by Obermeier ("Centralblatt," 1873, p. 145) in the blood of patients suffering from recurrent fever, shortly before or during the crisis, but their nature is unknown. See also Burdon Sanderson, "Brit. Med. Journ.," vol. ii. 1877, vol. i. 1878. Nedvetski (idem, 1872, p. 234) has seen moving particles, apparently derived from the white corpuscles, and bacteridia in the blood of choleraic patients. Nepveu ("Gaz. Med. de Paris," 1872, No. 3) has noticed bacteria in cases of erysipelas. Lewis (Pamphlet, 1872, "Lancet," 1873, 1, 446) has described a peculiar kind of Filaria, as being constantly present in large numbers in the blood of patients (in India) suffering from chyluria; Riess (Reichert's "Archiv," 1872, p. 237), bright granules in scarlet fever; Birsch-Hirschfeld ("Archiv d. Heilkunde," xiii. 1872, p. 38), micrococci in pyæmia and puerperal fever; Hüter ("Centralblatt," 1868, p. 177), similar forms in diphtheritis. See also Orth, "Archiv d. Heilkunde," 1872, xiii. p. 265, and Hiller, "Centralblatt," 1874, p. 833. In the "Biennial Retrospect of Physiology," of the New Syd. Soc. for 1875, several other references will be found. Considerable interest attaches to a statement recently made by Lostorfer ("Wien. Med. Jahrb.," 1872, Heft i. p. 96), and confirmed by Stricker, though vehemently denied by others, that the blood of syphilitic patients can be recognised by the presence of small bright bodies, which present Brunonian movements, and in the course of a week after removal from the body, enlarge, sprout, become vacuolated, and die. Lostorfer's statements have been partially corroborated by Biesiadecki, who, however, regards the bright particles as paraglobulin ("Untersuch. aus dem Path.-Anatom. Institute in Krakau," Vienna, 1872) precipitated by carbonic acid developed during the decomposition of the blood. Such particles are present in small numbers in all blood, but are uncommonly abundant in blood preparations from syphilitic patients, either because their blood contains more paraglobulin or less fibrinogenous substance than other blood. See article by Klein in "Lond. Med. Record," April 9, 1873. Halford, "On the Condition of the Blood after Snakebite," 1867, has observed peculiar nucleated cells in the blood after snakebite, which he believes to be derived from germinal matter in the poison of the snake, and to have grown at the expense of the blood.

see how any considerable alteration which affects its *physical* conditions merely, may thereby produce a most serious disturbance in the regularity of the circulation, and in the functions to which it ministers. Thus, it has been shown by the experiments of Poisseuille,* that a certain degree of viscidity is favourable to the motion of liquids through capillary tubes; a thin solution of sugar or gum being found to traverse them more readily than pure water will do. Hence any serious alteration in the proportion of the organic and saline compounds dissolved in the liquor sanguinis, and especially in that of the Fibrin, might be expected to produce obstruction in the capillary circulation, and to favour transudation of the fluid portion of the blood; and the numerous experiments of Magendie (Op. cit.) seem to favour this view, although they are far from manifesting that character for accuracy and discrimination, which would be required to afford an authoritative sanction to it. A much more determinate influence, however, must be exerted upon the Red Corpuscles, by any cause which seriously affects the specific gravity of the liquor sanguinis; and the perfect elaboration of the Albuminous constituent of the serum has been shown to be requisite to prevent it from copiously transuding the membranous walls of the vessels which it traverses.—These and other physical and chemical relations of the blood are quite subordinate to its vital reactions; and it is into them that we have now to inquire.

CHAPTER VIII.

OF THE CIRCULATION OF THE BLOOD.

1. *Of the Circulation in General.*

211. The Circulation of nutritive fluid through the body has for its object, on the one part, to convey to every portion of the organism the materials for its growth and renovation, together with the supply of Oxygen which is requisite for its vital actions (especially for those of the Nervo-Muscular apparatus); and at the same time to carry-off the particles which are set free by the disintegration or 'waste' of the tissues, and which are to be removed from the body by the Excreting processes. Of these processes, the one most constantly in operation, as well as most necessary for the maintenance of the purity of the blood, is the excretion of Carbonic Acid through the Respiratory organs; and this is made subservient to the introduction of Oxygen into the system. In Man, as in other Vertebrated animals, there is a regular and continuous movement of the nutritive fluid through the sanguiferous vessels; and upon the maintenance of this, the activity of all parts of the organism is dependent. In common with Birds and Mammals, again, Man has a Respiratory circulation entirely distinct from the Systemic; all the blood which has returned from the body being transmitted to the lungs, and being brought back to the heart again, before it is sent-forth afresh for the nourishment of the tissues and for the maintenance of their functional activity. The Heart is placed at the junction of these two distinct circulations, which may be likened to the figure 8; and it may be said to be formed by the fusion of two distinct organs, a 'pulmonary' and a 'systemic' heart; for its right and left sides, which are respectively appropriated to these purposes, have no direct commu-

* See M. Magendie's "Leçons sur les Phénomènes Physiques de la Vie," tom. iv. p. 57.

nication with each other (in the perfect adult condition, at least), and seem merely brought together for economy of material.* Each system has its own set of Arteries or efferent vessels, and of Veins or afferent trunks; these communicate at their central extremity by the Heart, and at their peripheral extremity by the Capillary vessels, which are nothing else than the minutest ramifications of the two systems, inosculating into a plexus.—Besides the systemic and pulmonary circulations, however, there is another which is no less distinct, although it has not an impelling organ of its own. This is the 'portal' circulation, which is interposed between the venous trunks of the abdominal viscera and the Vena Cava, for the purpose of distributing that blood through the Liver, in which organ its newly-absorbed materials undergo assimilation, whilst its excrementitious matters are separated by the secreting process. The Vena Portæ, which is formed by the convergence of the gastric, intestinal, splenic, and pancreatic veins, subdivides again like an artery, so as to form a capillary plexus which extends through the whole substance of the liver; and the Hepatic vein, collecting the blood from this plexus, conveys it into the Vena Cava. Thus the *portal* circulation is grafted (so to speak) upon the *general* circulation, in precisely the same mode as the respiratory circulation is grafted upon it in Mollusca and Crustacea; and if the 'sinus' of the Vena Portæ had possessed contractile muscular walls it would have ranked as the proper heart of the portal system. The really arterial character of the Vena Portæ is well shown by comparing it with the Aorta of Fishes; which is formed by the convergence of the Branchial veins, and then distributes the blood which it has received from them to the body generally.

212. That the movement of the Blood through the arterial trunks and the capillary tubes is, in Man, and in other warm-blooded animals, chiefly dependent upon the action of the Heart, there can be no doubt whatever. It can be easily shown by experiment, that if the arterial current be checked, the capillaries will immediately almost entirely cease to deliver the blood into the veins, and the venous circulation will be consequently arrested. And it has also been proved that the usual force of the Heart is sufficient to propel the blood, not only through the arterial tubes, but through the capillaries, into the veins; since even a less force will serve to propel warm water through the vessels of an animal recently dead.† But there are certain "residual phenomena" even in Man, which clearly indicate that this is not the whole truth; for not only is the general current of blood greatly modified in its passage through the circulating system, but there are many variations in its movement, which, being very limited in their extent, cannot be attributed to any central disturbance, and must therefore be dependent on causes purely local. Hence we are led to perceive that forces existing in the Blood-vessels themselves must have a considerable influence in producing both general and local modifications of the effects of the Heart's action. There are also indications of the existence of influences in which the blood-vessels do not partake, arising from those changes occurring between the blood and the tissues, that constitute the processes of Nutrition, Secretion, &c. Of the nature of these influences, and of the degree of their operation, the most correct idea may be obtained by examining the phenomena of the Circulation in those beings, in which the moving power is less concentrated than it is in the higher Animals. Thus we find that in Plants and the lowest animals, as in the earliest embryonic state of

* At an early period of fœtal life, as in the permanent state of the Dugong, the heart is so deeply cleft, from the apex towards the base, as almost to give the idea of two separate organs. † See Dr. Williams's "Principles of Medicine," 2nd edit., p. 185, *note*.

the highest, a movement of nutritious fluid takes place through a system of minute passages or channels excavated in the tissues (representing a *capillary* plexus), without any *vis a tergo* derived from an impelling organ. Ascending a little higher in the series, we meet with a system of vascular *trunks*, distributing the blood to these plexuses, and collecting it again from them; and the walls of these trunks are so far endowed with contractility, as to assist, by a sort of peristaltic movement, in the maintenance of the current through them. Still passing upwards, we find this contractility manifesting itself especially in some limited portion or portions of the vascular system, which execute regular movements of contraction and dilatation; and this tendency to concentration is increasingly observed, until the whole movement is subordinated to the action of a principal propelling organ, the Heart.*

213. The heart is contained in a serous sac named the *Pericardium*, by which its movements are facilitated. This sac is of conical shape with the base downwards, and rests on the diaphragm, to which it is firmly attached. It presents a *visceral* layer, which closely invests the muscular substance of the heart and is continued for some distance over the large vessels; and a *parietal* layer, which is reflected from the vessels and is greatly strengthened by fibrous tissue. The internal and opposed surfaces of the two layers are lined by pavement epithelium; the subserous layer contains a variable amount of fat and numerous lymphatics, in connection with which no stomata have been observed. *Nerves*, proceeding from the right vagus† just below the origin of the recurrent nerve, and from the phrenic, especially from those of the right side, have been traced into the parietal layer of the pericardium. The elaborate dissections of Dr. J. B. Pettigrew‡ have shown that the walls of the ventricles of the heart are composed of a series of seven layers or strata of muscular fibres, of which three are external, the fourth is central, and the remaining three are internal. The direction of the fibres constituting these layers gradually changes from a nearly vertical to a horizontal or transverse one, which is the course pursued by the fourth layer, and from this back again to a nearly vertical one. The fibres composing corresponding external and internal layers, such as layers one and seven, two and six, &c., are continuous in the left ventricle at the left apex, and in the right ventricle in the track for the anterior coronary artery, the fibres of both ventricles being for the most part continuous likewise at the base, forming, therefore, a series of figure-of-8 loops. The outermost fibres of both ventricles, on reaching the apex of the heart, present two bundles, which, curving round in the form of a vortex, or whorl, become continuous with the fibres of the carneæ columnæ and musculi papillares. Only the first and seventh layers are inserted into the auriculo-ventricular rings to which they pass in a direction almost at right angles to their planes. The object of these special arrangements appears to be, as Dr. Hensley§ has pointed out, to enable the muscular walls of the cavities of the heart to expel by their contraction the whole of their contents, whilst the shortening of the several fibres is both uniform in amount and moderate in extent.

214. There are, however, some important differences in the structure and

* See "Princ. of Comp. Phys.," chap. v. A very full and comprehensive account of the circulation and the apparatus by which it is effected in plants, in the lower animals, and in Man, will be found in Dr. J. Bell Pettigrew's work on the "Physiology of the Circulation," 1874.

† Luschka, quoted in Krause's "Histologie," 1876, p. 299, and in Frey's "Histology," Barker's translation, 1874, p. 403.

‡ "Phil. Trans.," part iii. 1864, p. 445.

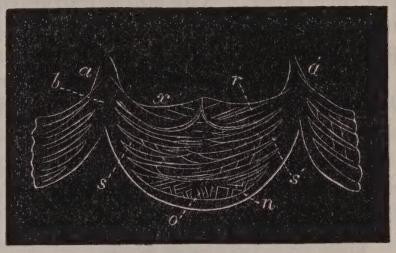
§ "Journ. of Anat. and Physiology," vol. iv. 1870, p. 83.

functional actions of the two divisions of the Heart, which should be here adverted to.—The walls of the *left* Ventricle are considerably thicker than those of the *right;* and its force of contraction is much greater. The following are the comparative results of M. Bizot's measurements,* taking the average of Males from 16 to 79 years:—

	Base.	Middle.	Apex.
Left Ventricle	$4\frac{1}{6}$ lines	... $5\frac{1}{6}$ lines	... $3\frac{3}{4}$ lines.
Right Ventricle	$1\frac{15}{16}$ lines	... $1\frac{3}{8}$ lines	... $1\frac{1}{30}$ lines.

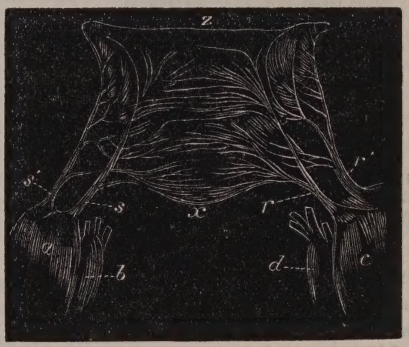
In the Female, the average thickness is somewhat less. It will be seen that the point of greatest thickness in the *left* Ventricle is near its middle; while in the *right*, it is nearer the base. The thickness of the former goes on increasing during all periods of life, from youth to advanced age; whilst that of the latter is nearly stationary. During pregnancy there is an hypertrophy of the left Ventricle to the extent of 1-4th or even 1-3rd of the original thickness of its walls.† The *left* Auricle is somewhat thicker than the *right;* the average thickness of the former being, according to Bouillaud, a line and a half; whilst that of the latter is only a line. In regard to the relative capacities of the right and left cavities, much difference of opinion has prevailed;† and so much fallacy may arise from the peculiar condition of the animal at the moment of death, that it is almost impossible to make any direct measurement.—The average capacity of the several cavities may, however, be estimated as equal in the full-sized Heart, each holding about five ounces.—The regurgitation of the blood is effectually prevented by *valves* which are situated between the cavities of the auricles and ventricles, and at the commencement of the aorta and pulmonary arteries. The right auriculo-ventricular aperture is guarded by the "tricuspid," and the left by the "mitral" valve; whilst the name "semilunar" valves is applied to those which are situated at the origin of the great arteries. These valves are composed of connective tissue with a layer of elastic tissue, which is a prolongation of the endocardium. The cuspidate valves contain a few striated muscular fibres, some of which run parallel

Fig. 116.



Segment of human semilunar valve from the pulmonary artery suspended from the fibrous band *a*, *a'*. *x*. *r*. Lunulæ, which when the valve is in action become accurately applied to corresponding lunulæ in the two remaining segments. *c*, Corpus Arantii, or portion usually thickened in old, though not in young people; *n*, thickened convex border attached to fibrous ring of pulmonary artery; *o*, thinner portion of segment. *s s'* Fibrous bands which break up in the mesial line of the segment to support and strengthen it.

Fig. 117.



Anterior segment of the human mitral valve, showing the threefold distribution of the chordæ tendineæ from above downwards, and from the mesial line towards the margins of the segments. *z*, Base of segment, *x*, apex ditto, *r r' s s'*, chordæ tendineæ from anterior portions (*a c*) of right and left musculi papillares, bifurcating and losing themselves in margins of segments. *b*, *d*, Posterior portions of right and left musculi papillares which send chordæ tendineæ to posterior segment of mitral valve.

* "Mém. de la Soc. Médic. d'Observation de Paris," tom. i.

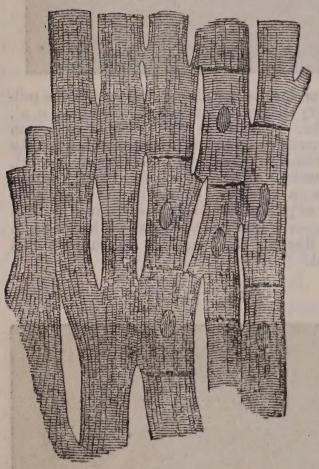
† Larcher, "Comptes Rendus;" Henle and Meissner's "Bericht," 1857, p 467.

‡ Winslow, Senac, Haller and Lieutaud, Boyer, Bizot and Legallois maintain that the

to the base, whilst others radiate from the fibrous ring.* In the case of the valves of the pulmonary artery they appear to be not quite equal in size, nor are they exactly upon the same plane; when made to act by pouring water into them, and watching them from below, it may be seen, according to Dr. Pettigrew, that the smallest segment, which is situated highest, descends with a spiral movement, and first falls into position; the middle-sized segment, which is placed a little lower, descends in like manner, fixing the first segment by one of its lunulæ or crescentic surfaces; the third and largest segment, which occupies a lower position than either of the others, descends spirally upon the crescentic margins of the other two, wedging and screwing them more and more tightly into each other. The spiral movement is occasioned by the direction of the sinuses of Valsalva, which curve towards each other and direct the blood in spiral waves upon the mesial line of each segment.

The *muscular fibres* of the heart are peculiar in presenting an intermediate form between the striped and unstriped varieties of muscular tissue; the fibres are smaller, and their striation is less strongly marked and less regular than those of ordinary striated muscle. This arrangement explains to some extent the uniformity and continuity of the cardiac movements. There is no trace of sarcolemma, and according to Eberth† the fibres are composed of broad quadrangular cells that are often forked at their extremities or give off lateral prolongations which are firmly adherent to each other. In a chemical point of view the muscular tissue of the heart is characterized by containing a larger amount of water than other muscles (79, instead of 76 per cent.); a considerable quantity of a peculiar kind of sugar, inosite, a very small proportion of kreatin, and a large amount of kreatinin.‡ The *nerves* of the heart are partly derived from the cerebro-spinal system, and partly from the sympathetic system. The two sets of fibres communicate in the cardiac plexus. The *cardiac plexus* receives branches, varying from one to three or more, from the trunk of the vagus on each side; a branch from the external laryngeal branch of the superior laryngeal, and one from the inferior laryngeal nerve of each side, and a branch from each of the cervical and the first dorsal ganglia of the sympathetic, though these vary greatly in size, and one is sometimes apparently wanting on one side.§ In addition, a few fibres are probably derived from the hypoglossal. Minute ganglia and ganglionic cells are distributed in the substance of the muscles, and lie also in the auriculo-ventricular and interventricular furrows. Some of

Fig. 118.



Anastomosing muscular fibres of the Heart seen in longitudinal section. On the right the limits of the separate cells with their nuclei are exhibited somewhat diagrammatically.

disparity in the size of the Auricles and Ventricles is considerable; Laennec, Cruveilhier, Gordon, Bouillaud, Meckel, and Portal that it is trifling; Lower, Sabatier, Weiss, Andral, and more recently Pettigrew, that there is no difference whatever.

* See Pettigrew, "Transact. of the Roy. Soc. of Edinb.," vol. xxii. 1864, p. 761; Gussenbauer, "Ueber die Muskelatur der Atriovent. Klappen des Menschenherzens, Wiener Sitzber." Band lvii. 1872.

† Virchow's "Archiv," Band xxxvii. Heft 1, p. 100. See also Schweigger-Seidel, Stricker's "Histology," New Syd. Soc. Trans. vol. i. p. 248.

‡ Ranke, "Grundzüge d. Physiolog.," 1868, p. 307.

§ See Heule, "Anatomie, Nerveulehre, p. 572.

the ganglionic cells resemble those of the sympathetic in giving off from one and the same pole a straight and a spiral fibre; others are bipolar; and others again form bi-celled ganglia, resembling two pears applied to each other by their broad ends, the stalks representing the nerves they give off. These have no spiral fibre. The precise mode of termination of the nerve fibres has not been made out, but they probably lose their double contours, and continuing their course as pale fibres form loops and anastomoses around the muscle cells.* It will be observed that in consequence of the absence of a sarcolemma the ultimate nervous plexus is in immediate contact with the contractile substance. The cavities of the Heart are lined by the 'endocardium' in which all the layers of a vascular wall are represented—viz., a single layer of endothelial cells, a stratum of fine elastic fibres, and a layer of connective tissue in which are distributed many unstriated muscle-fibre cells, for the most part arranged longitudinally. A rich plexus of nerves has been observed in it. According to Eberth and Belajeff,† the endocardium, especially in the ventricles, presents a mesh-work of fine *lymphatics*, the walls of which in some parts consist only of a single layer of intimately-adhering cells. No lymphatics are traceable on the chordæ tendineæ, and very few upon the auriculo-ventricular and semilunar valves. We shall now examine what agency in the Human Circulation may be attributed to the Heart, the Arteries, and the Veins respectively; and what other forces may be fairly presumed to operate in the Capillary circulation.‡

2. *Action of the Heart.*

215. The Heart is endowed in an eminent degree with the property of *Irritability*, by which is meant the capability of being easily excited to movements of contraction alternating with relaxation. Thus, after the Heart has been removed from the body and has ceased to contract, a slight irritation will cause it to execute, not one movement only, but a series of alternate contractions and dilatations, gradually diminishing in vigour until they cease. The contraction begins in the part irritated, and then extends to the rest. It appears, however, from Sir James Paget's experiments,§ that it is necessary for the propagation of this irritation, that the parts should be connected by muscular tissue which probably contains nerve fibres and of which a very narrow isthmus will suffice; the propagation will not take place if the connecting isthmus be composed of a portion of the auriculo-ventricular ring, which has been supposed by some to be peculiarly efficacious in this conduction.‖ Like the contractility of other muscles, that of the Heart can only be continuously sustained by a supply of arterial blood to its own tissue. This is shown not only by the serious effects produced by disease of the coronary arteries, but also by the experiments of Erichsen¶ and Schiff;** the former of whom found that ligature of the coronary arteries rapidly produced cessation of the movements of the heart, especially if the cardiac veins were also opened; whilst the

* Langerhans, Virchow's "Archiv," Band lviii. 1873, p. 71.

† Virchow's "Archiv," 1866, Band xxxvii. p. 55.

‡ Many of the phenomena of the circulation can be conveniently studied, and practice in the use of recording instruments, manometer, sphygmograph, kymographion, &c., obtained by means of an india-rubber model of the circulatory system constructed by Dr. Rutherford, and described in the Journal of "Anatomy and Physiology," vol. vi. p. 249.

§ "Brit. and For. Med. Review," vol. xxi. p. 551. See also Englemann, "Archiv f. d. gesammte Physiologie," Band xi. 465.

‖ Quinine in moderate doses appears to have a remarkable power of exalting the irritability of the heart, though in very large doses it depresses it. See Schtschepotjew, Pflüger's "Archiv," 1879, Band xix. p. 53.

¶ "Lond. Med. Gaz.," 1842, vol. ii. p. 561. ** "Arch. f. Phys. Heilk.," tom. ix.

latter obtained a local paralysis of either ventricle, according as the artery distributed to the one or the other was tied.* The contractility of the Heart is much less speedily lost in cold-blooded animals than in warm-blooded; the heart of a Frog, for instance, will continue to pulsate for as many as twelve hours after its removal from the body, particularly if kept in an atmosphere of oxygen, though it ceases in a few minutes if immersed in Carbonic acid gas.† It has further been shown by Mr. Tod, that the irritability of the heart is of great duration after death in very young animals; which, as was long since demonstrated by Dr. Edwards, agree with the cold-blooded Vertebrata in their power of sustaining life for a lengthened period without oxygen. That the heart in dilating exerts a distinctly marked suction power is shown by the negative pressure indicated by a manometer introduced into the auricles or ventricles. This negative or minus pressure in the auricles has long been known, but more recently it has been accurately measured.‡ Experiments show that whilst during systole the pressure in the left ventricle is at its maximum, and is the same as that in the aorta, amounting (in three dogs) to from 114 to 142 mm.; the minimum pressure during diastole was – 52 mm. Hg. In the right ventricle the maximum pressure was + 62 mm. Hg, and the minimum pressure was – 17·2 mm. Hg. In the right auricle its maximum pressure was 20 mm. Hg, and the minimum pressure – 11·2. That these minus quantities do not depend on inspiration is rendered evident by the fact that a negative pressure of – 23·5 mm. Hg was still observed after the thorax had been opened, and artificial respiration maintained.§ It is uncertain whether the suction power of the cardiac cavities is due to active muscular elongation, or to the elasticity of the walls of the thick masses of muscle striving to resume their hollow form after contraction.

216. The most reasonable explanation of the cause of the contractions of the heart is that which attributes them to the continuous excitation that the blood flowing through the cavities exerts on the cardiac excito-motor ganglia. This meeting with continuous resistances in the cardiac inhibitory ganglia—only periodically, that is to say, after overcoming such opposition—acts on the muscular tissue. Bowditch‖ has shown that the apex of the heart, when separated from the rest of the organ by a ligature or compression, remains absolutely at rest; or if, as occasionally occurs, it begins to beat again, it is due to the restoration of an imperfectly destroyed connection between the apex and the motor apparatus at the base of the heart. As already stated, Schweigger-Seidel has observed a rich plexus of nerve fibres in this membrane, whilst its sensitiveness to mechanical irritation was incidentally shown by an experiment of Bernard,¶ in which the contact of the bulb of a thermometer with the interior of the ventricles immediately increased the number of pulsations. Schiff** and Budge†† have, moreover, shown that the action of both auricles and ventricles rapidly ceases if they are placed on blotting-paper; but that they may be called into action again, either by immersing them in blood, or by dropping a little blood into their cavities. And an ingenious experiment was made by Haller himself, showing that if arrangements are made, by which either the right or left side of the Heart remains filled with blood

* v. Bezold, however, found that ligature of the coronaries produced but little effect for a considerable period in rabbits. † Castell, Müller's "Archiv," 1854, p. 226.

‡ G. F. Goltz and J. Gaule, Pflüger's "Archiv," Band xvii. p. 100.

§ For some evidence that an impression of active dilatation is caused by the injection of the coronary arteries, see A. H. Garrod in "Nature," Fig. 19, 1874.

‖ Foster's "Journ. of Physiol.," vol. i. 1878–9.

¶ "Leçons sur les Liquides de l'Organisme," 1859, p. 124.

** Vierordt's "Archiv," 1850, p. 34. †† "Archiv f. Phys. Heilk.," 1846, p. 561.

whilst the other can discharge its contents and remains empty, that side which is stimulated by the presence of the blood continues to beat rhythmically long after the movement of the other had ceased. When the irritability of the heart is nearly exhausted, the usual *rhythm* is often a good deal disturbed, so that the contractions of the auricles and ventricles do not regularly alternate with each other; and one set frequently ceases before the other.

217. When the Heart is exposed in a living animal and its movements are attentively watched, they are seen to follow each other with great regularity. In an active and vigorous state of the circulation, however, they are so linked together, that it is not easy to distinguish them into periods; both Auricles contracting, and also dilating, simultaneously; and both Ventricles doing the same. The *systole* or contraction of the Ventricles corresponds with the projection of the blood into the arteries; whilst the *diastole* or dilatation of the Ventricles coincides with the collapse of the arteries. The contraction of the Auricles and Ventricles run into each other, that of the Auricle immediately preceding that of the Ventricle. The entire period that intervenes between one pulsation and another is nearly equally divided between the systole and diastole of the Ventricles, but the division is very unequal as regards the Auricles; about one-fifth of the whole being occupied in their contraction, and the remainder being taken-up by their dilatation.* The following tabular view will perhaps make the relations of the several parts of this series more intelligible:—

Auricles.		Ventricles.	
$\frac{4}{5}$	Dilatation.	Contraction.	$\frac{2}{5}$
	Continued Dilatation.	First stage of Dilatation.	$\frac{2}{5}$
$\frac{1}{5}$	Contraction.	Second stage of Dilatation.	

In some very careful experiments, Donders† ascertained that in different persons in whom, when at rest, the pulse varied from 74 to 94 per minute, the duration of the systole of the ventricles—*i.e.*, from the commencement of the first to the commencement of the second sound—varied from 0·327 to 0·301 of a second, and that it constituted from 40·6 to 45·6 per cent. of the time occupied by an entire cardiac revolution. In a man whose pulse was only 32 per minute, the duration of the ventricular action was still 0·307 to 0·325 of a second, though its proportion to the whole revolution had fallen to about 18 per cent. From whence it appears that the duration of the activity of the Ventricles, determined by the ganglia of the heart itself, is independent of the duration of the entire cardiac revolution, which is regulated by the Pneumogastrics.‡ Landois,§ who has paid much attention to the subject, finds the

* See Marey, "Circulation du Sang," Paris, 1863, p. 68.

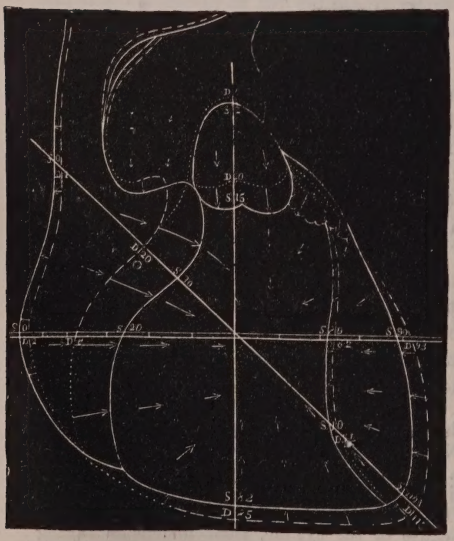
† "Nederlandsch Archief voor Genees- en Natuur-kunde," 1866, p. 139, of which paper a full translation is to be found in the "Dub. Quart. Journ.," vol. xlv. p. 225. See also some estimates by Landois, Henle and Meissner's "Bericht," 1866, p. 411. By some (Brücke, "Vorlesungen, a. d. Physiologie," 1874, p. 180) it has been supposed that the injection of the coronary arteries is the cause of the systole, their distension taking place during the diastole of the ventricle in consequence of the mouths of those vessels being covered during the systole by the semilunar valves; but careful examination has shown that the mouths of the coronary are, in a very large number of cases, above the level of the semilunar valves, and vivisection has shown that the coronary arteries when divided yield a jet synchronously with the systole. See Hyrtl, "Wiener Sitzungsber.," Band xiv. p. 73, and "Neb. d. Selbststeuerung des Herzens, Wien," 1855.

‡ See Sibson, "Medical Anatomy," 1869, and the instructive papers by Dr. Halford, now Prof. of Physiology at the Univ. of Melbourne, "On the Times and Manner of the Closure of the Auriculo-Ventricular Valves," and "On the Movements and Sounds of the Heart," Lond., 1861; also Pettigrew's Lectures on the 'Physiology of the Circulation,' "Edinb. Med. Journ.," 1873.

§ Landois, "Physiologie," 1879, p. 94.

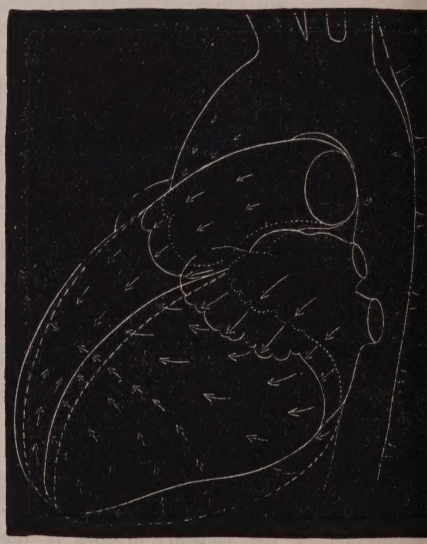
duration of the period *a b*, which includes the *pause and the systole of the auricles* (*a b*, Fig. 122), liable to considerable variation, and to be dependent on the number of the heart's beats in the minute, for of course the more quickly the heart beats the slower is the pause, and *vice versâ*. Even when the heart is beating slowly it is often impossible to distinguish between the horizontal line of the pause and the rise corresponding to the auricular systole. In one case, where the heart was beating 55 times in the minute, the pause lasted 0·4 second, and the auricular systole 0·177 second. In Fig. A, the pause + auricular systole (with a pulse of 74 per minute) lasted 0·5 second. In B the period *a b* (= 19–20 vibrations) lasted 0·32 second. The *Ventricular systole*, represented by the line *b*—*e*, persists from the beginning of the first to the beginning of the second sound. It is more constant than the preceding, but is shorter when the heart's action is rapid, longer when this is slow. In B it lasted 0·29 second. In a case when the pulse was 55 per minute it lasted 0·34, but with a very rapid pulse it may last only 0·199 second. It does not vary much in cases of great dilatation and hypertrophy of the ventricle. The *period* which elapses between *d* and *e*—that is to say, *between the complete closure of the aortic semilunar and of the pulmonary semilunar valves*—varies in proportion as the pressure in the aorta exceeds that in the pulmonary artery, and may therefore vary from an almost imperceptible period to 0·05 or 0·1 second. Lastly, the period in which the ventricles relax after closure of the

Fig. 119.



Front view of the movements of the heart in systole and diastole.

Fig. 120.



Profile view of the movement of the heart in systole and diastole.

valves represented by the line *e* to *f*, may on the average be estimated at 0·1 second. The extent and direction of the movements of the several parts of the heart in systole and diastole are well represented in Figs. 119, 120.*

* The outlines of the cavities of the heart, and the great vessels, are here indicated, at the end of the *systole* of the heart, by continuous lines—at the end of the *diastole* by interrupted or dotted lines. (The drawing and descriptions are taken from Dr. Sibson's admirable treatise on "Medical Anatomy," 1869, Col. 73. The dotted lines are less accurate than the interrupted lines.) The systolic movements are everywhere shown by arrows, the extent of

An entire cardiac revolution may be described in the following terms, commencing with the systole or contraction:—The Auricles and Ventricles are both filled with blood, which has flowed into them from the veins. The Auriculo-ventricular valves are open, and the arterial valves (both aortic and pulmonary) are perfectly closed. Commencing at the entrance of the great veins, a sudden contraction of the Auricles now takes place, which extends without appreciable pause in a peristaltic manner over the ventricles. By the contraction of the Auricles a portion of their contained blood is discharged into the Ventricles, completing the distension of these cavities, and effecting the closure of the Auriculo-ventricular valves which float up into contact. The Ventricles instantly contract tightly, closing the Auriculo-ventricular valves and forcing open the arterial valves, through which the blood is propelled into the arteries. The great arteries, now distended with blood, recoil on their contents and close the semilunar valves. As soon as the contraction of the Ventricles is completed, a sudden movement of relaxation takes place similar to that of an elastic bag when released from pressure, and this is followed by a brief interval of complete rest; during which both Auricles and Ventricles are rapidly filling with blood; contraction then again recurs. During the systole the heart becomes more globular, or, perhaps strictly speaking, more conical in form. The chief movement observable in the Auricles is the sudden retraction of the appendices, which almost instantly become refilled with blood as the ventricles contract. The contraction of the two ventricles seems to take place simultaneously towards a centre or point of rest, which in the right ventricle, where the action is most easily observed, is situated about the middle of its length, near the septum and opposite the attachment of the anterior papillary muscle (Sibson). The base of the heart descends rather more than the apex ascends. There is a slight twisting movement of the whole heart during the systole, both on its longitudinal and on its transverse axis. By its rotation on its transverse axis the apex of the heart is tilted forwards; by its rotation on the long axis the left ventricle, which during the diastole looks backward, is turned forwards. The combination of the two *movements* gives to the apex a twisting movement from left to right and forwards. The apex beat is felt between the 5th and 6th ribs, and is caused by a part just above the apex. In the act of contraction the heart may be felt to become hard. During the diastole the heart undergoes a change in form, the converse of that which has been above described. The *impulse* is felt over every part of the Ventricles during their contraction, but most forcibly over their centre. It is synchronous with the first sound of the heart, with the opening of the auriculo-ventricular valves, the dilatation of the aorta, the arterial pulse, and the jet of blood that occurs when an opening has been made through the walls of the ventricle. Senac and Hunter* attributed the impulse to the effort of the arch of the aorta to straighten itself when blood is forced into it by the systole of the heart, the aorta being the fixed point against the back, and the heart in some degree loose or pendulous, the influence

the movements being marked by the length of the arrows. As it is more difficult to watch and measure the movements of the heart from the side than from the front, the side view (Fig. 120) is not so accurate as the front view (Fig. 119). Brücke ("Vorlesungen," 1874, p. 172), whose experiments were made by implanting needles into the hearts of rabbits, and watching the reversed motions of the heads, maintains that all parts of the ventricles move downwards in systole with the exception of the apex, the amount of movement increasing from below upwards. Halford (op. cit.) believes the apex of the heart is drawn up towards the base, but nevertheless undergoes less change of position than any other part, its upward movement being neutralized by the descent of the whole heart occasioned by the elastic recoil of the great vessels springing from the base.

* "Hunter's Works," by Palmer, vol. iii. p. 185.

of its own action is thrown upon itself, and it is tilted forwards against the inside of the chest. Colin* and others have shown, however, that this cannot be the only cause, since the impulse is felt when all the vessels are compressed or tied, and it seems probable that it is chiefly, or in part, due to the shortening, tilting, and pressure of the heart against the parietes of the chest, which occurs in systole.

218. The course of the circulating fluid through the Heart, and the action of its different valves, will now be briefly described.—The Venous blood, which is returned by the ascending and descending Vena Cava, enters the *right* Auricle during its diastole, on the contraction of which it is propelled through the tricuspid valves into the Ventricle, which thus becomes completely distended. The reflux of blood into the veins during the auricular systole, is impeded by the contraction of their own walls, and is limited on the right side by the valves placed at the junction of the jugular and subclavian veins; but these valves are so formed as not to close accurately, especially when the tubes are distended; so that a small amount of reflux usually takes place, and this is much increased when there is any obstruction to the pulmonary circulation. Whilst the *right* Ventricle is contracting upon the blood that has entered it, the *carneæ columnæ*, which contract simultaneously with its proper walls, put the *chordæ tendineæ* upon the stretch, preventing the flaps of the Tricuspid valve from being driven back into the auricular cavity. The blood is now expelled by the ventricular systole into the Pulmonary artery, which it distends, passing freely through its Semilunar valves; but as soon as the *vis a tergo* ceases, and reflux might take place by the elastic recoil of the arterial walls, the valves are filled out by the backward tendency of the blood, and completely check the return of any portion of it into the ventricle. The blood, after having circulated through the lungs, returns as Arterial blood, by the Pulmonary veins, to the *left* Auricle; whence it passes through the Mitral valve into the *left* Ventricle, and thence into the Aorta through its Semilunar valves in the same manner with that on the other side, as just described.† There is a well-known anatomical difference between the auriculo-ventricular valves on the two sides, which has given rise to the diversity of name; and this seems, from the researches of Mr. King,‡ to be connected with an important functional difference. The Mitral valve closes much more perfectly than the Tricuspid; and the latter is so constructed as to allow of considerable reflux, when the cavities are greatly distended. According to Dr. Flint,§ an equally well-marked difference in sufficiency also exists between the arterial semilunar valves on the two sides, the closure of the pulmonary being much less perfect than the aortic. Many occasional causes tend to produce an accumulation of blood in the venous system, and in the right side of the Heart; thus, any obstruction to the pulmonary circulation, cold, compression of the venous system by muscular action, &c., are known to favour such a condition. This is a state of peculiar danger, from a liability which over-distension of the Ventricular cavity has to produce a state of muscular paralysis; and in the structure of the Heart itself there seems, as just stated, to be a provision against it. For, when the ventricle is thus distended, the Tricuspid valves do not close properly; and a reflux of blood is permitted, not only into the Auricle, but also (through the imperfect closure of their valves under the same circumstances) into the large

* "Physiologie comparée," 1873, t. ii. p. 390. See also Rosenstein, "Deutsch Archiv f. Klin. Med.," Band xxiii. p. 79.

† For a full account of the mechanism of the Semilunar valves of the Heart, see Ceradini, abstract in "Centralblatt," 1872, pp. 123 and 135.

‡ "Guy's Hospital Reports," vol. ii. § "Physiology," 1866, p. 203.

veins. This is proved by the fact, several times observed by Dr. J. Reid in his experiments upon Asphyxia, &c., that when the action of the right ventricle had ceased from over-distension, he could frequently re-excite it, not merely by puncturing its walls, but by making an opening in the jugular vein.* This fact evidently affords an indication of great importance in the treatment of Asphyxia; and it explains the reflux of blood, or *venous pulse*, which is frequently observed in cases of pulmonary disease, and which, according to Mr. King, always exists even in health, though in a less striking degree.†

The movements of the blood through the heart and large vessels contained in the chest is to some extent influenced by the respiratory acts. Whilst a full inspiration is taken, not only does air enter through the trachea, but blood enters through the great veins to fill the vacuum which the descent of the diaphragm tends to produce. Were it not for the valves and for the greater strength of their coats it would also enter by the arteries. The auricles become distended, and do not at first deliver their blood freely to the ventricles, and the pulse is therefore feeble and small, though after a short time it becomes stronger and fuller. In extreme expiration, on the contrary, the chest cavity is diminished in size; the lungs, and with them the heart, are compressed, hence little blood enters the heart in diastole, and little is driven out; therefore the systole and the pulse at the wrist are feeble. The alternate expansion and contraction of the chest cavity which occurs in normal respiration is most favourable to the circulation, for there is then a certain tendency to dilatation of the cardiac cavities during diastole, and yet there is no interference with the discharge of the blood during systole. If, instead of allowing the glottis to remain open after a deep inspiration it is closed, and a strong expiratory effort be made (Valsalva's experiment), the cavities of the heart may be so compressed that the current of blood is arrested. Blood enters the heart with difficulty, as is shown by the swelling of the veins of the neck, and this little passes rapidly through the expanded lungs into the left Ventricle, which quickly discharges it. The lungs and heart then are both empty, and the cardiac sounds and pulse may almost or quite cease. If, on the contrary, a full expiration be made, and the glottis being closed, a strong inspiratory effort be made, the cavities of the right heart become distended; for the elastic traction of the lungs is exerted and the rarefaction of the air in the chest promotes the entrance of blood through the great veins, the lungs become filled with blood, whilst but little blood enters the left heart, and hence again the pulse becomes small or imperceptible. The pulmonary or intra-thoracic circulation is aided by the elastic traction exerted by the lungs, for the blood in the capillaries of the lungs moves under the pressure of the air in the lungs; whilst that in the pulmonary veins moves under a lower pressure, because the elastic traction of the lungs, by tending to dilate the left auricle, must operate favourably to the discharge of the blood from the capillaries into the left auricle. The elastic traction of the lungs upon the right ventricle, and consequently upon the movement of the blood through the pulmonary artery, is exerted to a less extent on account of its strength.

* "Physiol., Anatom., and Pathol. Researches," chap. iii.

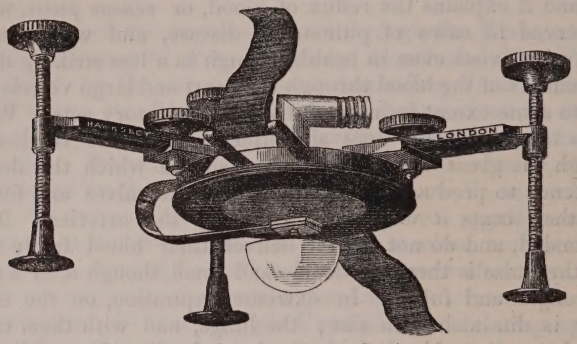
† Dr. Herbert Davies ("Proceed. Roy. Soc.," No. 118, 1870, and pamphlet) maintains that the four chief orifices of the heart are circular in form and constant in area during the entire periods of systole and diastole, and that they bear an exact mathematical relationship to each other, expressed by the formula—

$$\frac{\text{Area of tricuspid}}{\text{Area of mitral}} = \frac{\text{Area of pulmonic}}{\text{Area of aortic}}$$

but his conclusions have been controverted on mathematical grounds by Mr. Trotter, "Journ. of Anat.," 1870, p. 298.

The experiments of MM. Chauveau and Marey,* with a peculiar form of Cardiograph, represented in Figs. 121, 123, in which levers of extreme lightness register the undulations of the air contained in elastic sacs applied to the surface of the Heart and Thorax, show clearly the sequence and duration of

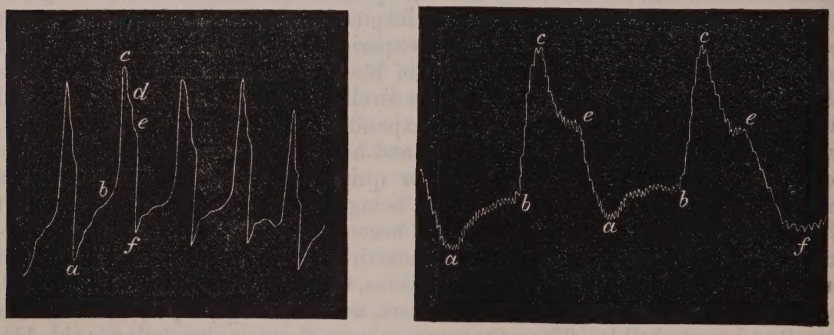
FIG. 121.



Marey's drum for registering Cardiac impulses.

the movements of the Auricles and Ventricles, and the coincidence of the *impulse* with the contraction of the Ventricles (Figs. 122, 124). The Cardiograph, as modified by Sanderson, consists of a hollow disc of brass, the front

A FIG. 122. B



Cardiac Impulse Tracings.

A. Normal curve of Cardiac Impulse of Man.

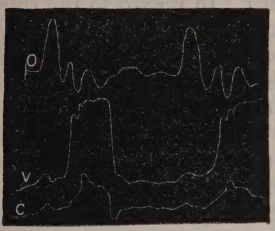
B. Normal curve of Man registered on a vibrating tuning-fork plate. Each undulation corresponds to 0·01613 of a second. In both tracings *a*, *b*, represents the systole of the auricle; *b*, *c*, the systole of the ventricles; *d*, the closure of the aortic valves; *e*, closure of the pulmonary valves; *e*—*f*, diastole of the ventricle.

of which is closed by a thin india-rubber membrane called a tympanum. To the brass back a flat steel spring is screwed, which is bent twice at right angles in such a way that its extremity is opposite the centre of the tympanum. The extremity is perforated by a steel screw, the point of which rests on the membrane, whilst its head is surmounted by an ivory knob. The tympanum is provided with three adjusting screws, by which when in use it rests on the wall of the chest with its face parallel to the surface, and can be approximated or withdrawn at will. The cavity of the disc communicates by a vulcanized india-rubber tube with a second tympanum represented by *b* in

* "Annal. des Scien. Nat.," 4th sér., Zool., tom. xvii. p. 374; and "Mém. de la Soc. de Biol.," sér. iii. tom. iii. pt. ii. 1862, p. 1. For other Cardiographic tracings and accounts of the instruments employed, see A. H. Garrod in "Journ. of Anat. and Phys.," Nov. 1870, and Rutherford's Lectures in "Lancet," 1871–2.

Fig. 123, in such a way that the two tympana and the tube enclose an air-tight cavity. The movement of the second tympanum is magnified and inscribed on a registering cylinder by a lever. The causes of the impulse according to Sibson are, first—the rigidity of the muscular walls during contraction; secondly, a lever movement forward, due to the thickening of the muscle, which occurs during contraction, being resisted by the fibrous bed of the pericardium on which the heart rests; and, lastly, the outward pressure of the blood in the ventricles on the walls by which it is expelled, and through those walls on the ribs and intercostal spaces.

Fig. 124.



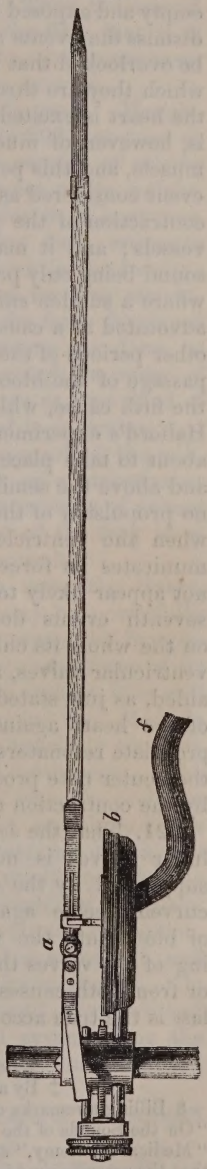
Tracing obtained by the Cardiograph of MM. Chauveau and Marey.

In this tracing *o* represents the short and abrupt contraction of the Auricles which immediately precedes the more energetic and protracted contraction of the Ventricles, represented by the line *v*. The line *c* shows the impulse of the Heart to be coincident with the Ventricular contraction.

219. When the ear is applied over the cardiac region, during the natural movements of the Heart, two successive *sounds* are heard, each pair of which corresponds with one pulsation; there is also an *interval of silence* between each recurrence, and the sound that immediately follows this interval is known as the *first* sound, the other as the *second*.—The *first* sound is dull and prolonged, and is heard all over the left ventricle with equal intensity; it is evidently synchronous with the impulse of the Heart against the parietes of the chest, and also with the pulse, as felt near the heart; it must, therefore, be produced during the Ventricular Systole.—The *second* sound, which is short and sharp,* follows so immediately upon the conclusion of the first, that it cannot take place during the auricular systole as some have supposed, but must be assigned to the first stage of the ventricular diastole, when the auricles also are dilating.

220. The causes of the sounds, and more especially of the *first*, have been the subjects of much discussion. A number of very distinct actions are taking place during the period of the production of the latter; and each of these has been separately fixed on as competent to produce it. Thus, we have (1) the impulse of the heart against the parietes of the chest; (2) the contraction of the muscular walls of the ventricles; (3) the rush of blood through the narrowed orifices of the aorta and pulmonary artery; (4) the general molecular collision of the particles of the blood amongst each other, and their friction against the walls of the ventricles; (5) the sudden collision of the stream of blood issuing from the ventricles with the column of blood at rest on the semilunar valves of the aorta and pulmonary artery; (6) the friction of the heart against the pericardium; (7) the vibration of the walls of the chest from the sudden rigidity and pressure of the

Fig. 123.



Marey's apparatus for registering Cardiac impulses.

* The difference between these two sounds is well expressed (as Dr. C. J. B. Williams has remarked) by articulating the syllables lubb, dŭp.

heart; and (8) the sudden tension of the valves of the auriculo-ventricular orifices. In regard to the first event, it may be remarked that excellent observers, as Ludwig and Dogiel,* Sibson and Broadbent, maintain that though much reduced in intensity the first sound is still audible during the contractions of an empty and exposed heart and after removal of the chest walls, which enables us to dismiss the events numbered above, 1, 4, and 5, as efficient causes. It must not be overlooked that the *susurrus* of ordinary muscles is due to the vibration into which they are thrown during contraction, whilst Marey has shown that when the heart is excited to contract the shortening of the fibres is a single act. It is, however, of much longer duration than the contraction of ordinary striated muscle, and this perhaps enables it to be perceived.† In regard to the third event considered as a cause, it has been well remarked,‡ that there is no abrupt contraction of the passages through which the blood flows from ventricles to vessels; and it may be added, that there would be no sound if there were; sound being only produced at that point in a vessel conveying a stream of fluid, where a sudden *enlargement* occurs. In regard to the fourth event, strongly advocated as a cause by Sibson and Broadbent, it may be argued that during other periods of the heart's rhythm, such collision produces no sound, as in the passage of the blood from the auricles to the ventricles; and in reference to the fifth cause, which has been advanced by Dr. Leared, it appears from Dr. Halford's experiments, that at the moment when the systole of the ventricle is about to take place, the active and passive columns of blood, or those below and above the semilunar valves, are not separated by any space; that there is no propulsion of the blood from a distance against the passive column, but that when the ventricles contract, the fluid pushes open the valves and communicates its force to the column in the vessels, a circumstance which does not appear likely to be accompanied by much, if any sound. The sixth and seventh events doubtless aid in the production of the first sound, but on the whole its chief factors appear to be the sudden tension of the auriculo-ventricular valves, and the contraction of the muscular walls of the ventricle, aided, as just stated, by the vibration of the walls of the chest, and the friction of the heart against them.§ Wintrich,‖ indeed, states that by the aid of appropriate resonators he has been able in the first sound to discriminate between the acuter note produced by the valvular tension from the deeper sound caused by the contraction of the muscle.¶

221. That the *second* sound is produced in the act of closure of the semilunar valves is now almost universally admitted, since it is altogether suppressed by the simple act of hooking back one of these valves with a curved needle against the side of the artery so as to permit a reflux of blood into the ventricle. Whether it proceeds from the sudden tightening of the valves themselves, or from the recoil of the blood against them, or from both causes combined, has not been clearly determined; probably the last is the true account of it.—When the first sound is altered by disease of the

* Ludwig's "Arbeiten," 1868, p. 78.

† See Marchand, Pflüger's "Archiv," Band xv. p. 511.

‡ By a writer in the "Med.-Chir. Rev.," April, 1860, p. 354.

§ Billing's remarks upon this subject in his "Principles of Medicine," Halford's pamphlet "On the Sounds of the Heart," and the observations of Sibson and Broadbent in Sibson's "Medical Anatomy," are deserving of careful perusal. For some exceptional statements, as that the second sound is due to a contraction of the auricles, see Paton 'On Sounds of Heart,' in "Dub. Quart. Journ.," vol. xcix. p. 83, *et seq.* The various treatises on practical medicine and auscultation may also be referred to. Dr. Dunglison, "Human Physiology," vol. i. 1856, p. 397, has tabulated the opinions of a large number of authors. They exhibit an extraordinary amount of discordance upon a matter of pure observation.

‖ Hofmann and Schwalbe's "Jahresbericht," Band ii. 1873, p. 537.

¶ See also Arnold, "N. York Med. Journ.," April, 1878.

semilunar valves, occasioning obstruction to the exit of blood, the second sound also is affected in its character; and if the disease be of such a kind as to prevent these valves from effectually closing, a reflux of blood takes place into the ventricle at the time of its diastole, causing a rushing sound that is analogous to the ordinary first sound, or to some of its modifications. Thus, the second sound may come to acquire so completely the character of the first, that it is difficult to distinguish the two in any other way, than by the synchronousness of the first with the heart's stroke and with the pulse in the arteries.

The mechanical force put forth by the heart is wonderfully great. Haughton* estimates the total daily work of both Ventricles at 124·208 foot-tons, or admitting the weight of the heart to be nine ounces, it is capable of raising 20·576 pounds one foot in height per minute for every ounce of its weight, which considerably exceeds the work done by the muscles in a boat-race. Dr. Andrew Buchanan,† proceeding upon somewhat different data, estimates the force exerted by the heart per diem to be 42·3 foot-tons in the twenty-four hours. Helmholtz‡ calculates that the heart can raise its own weight, through 20,250 ft. in one hour, and Ranke§ estimates that the force developed by the left Ventricle alone amounts to 64,800 kilogrammeters per diem, or that it would be sufficient to raise 142,560 lbs. avoird. through the space of 39·37 inches; the force of the right Ventricle he estimates at one-third of the above. Whichever estimate is taken the power exerted is enormous, and greatly in excess of any effort of the muscles under the control of the will. Each systole of the heart is accomplished by a single shock or contraction or *sécousse*, and not by a series of shocks, as in the case of the muscles of animal life. The duration of the shock in the case of the heart of the frog is as much as fifteen times longer than that of ordinary striated muscle.

222. In regard to the influence of the Nervous system upon the Heart, there is abundant evidence to show that its movements may be powerfully affected by causes acting either upon the Cerebro-spinal or upon the Sympathetic system; and whilst, upon the one hand, the energy and force of its contractions may be augmented by stimuli applied to these centres, it is well ascertained that the Pneumogastric nerves, originating in the Medulla oblongata, are the means of conveying an influence of a precisely contrary nature, serving to inhibit, restrain, or regulate the Cardiac movements. The fact that the Heart will continue to beat after its removal from the body, or after the *gradual* removal of the whole Cerebro-spinal axis, especially if the flow of blood through the Lungs be kept up by artificial respiration,‖ as well as the existence of anencephalic monsters which possess a regularly-pulsating heart, clearly show that this organ is not exclusively or *essentially dependent* upon the central nervous system for the continuance of its rhythmical action. Its movements under these circumstances must be regarded as automatic, and governed by the Cardio-motor ganglia distributed through its substance. On the other hand, the well-known effects of mental emotions and of sudden and severe injuries of either the Sympathetic or Cerebro-spinal system upon the Heart's action, prove with equal certainty that its action may be influenced through nervous fibres in connection with those centres.

223. *Excito- or Cardio-motor System of the Heart.*—Careful dissections¶

* "Principles of Animal Mechanics," 1873, p. 145.

† "Lancet," 1870, vol. ii. p. 666. ‡ "Med Times and Gaz.," 1864, p. 529.

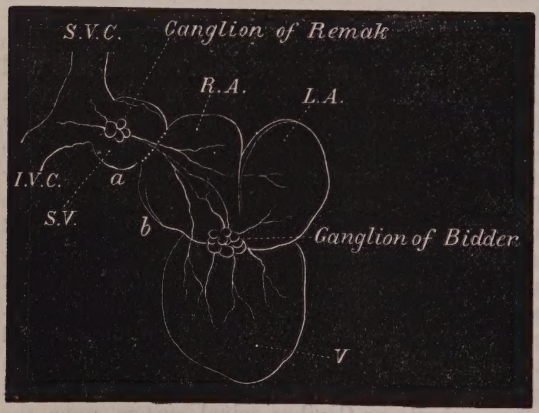
§ "Grundzüge der Physiologie," 1868, p. 332.

‖ See the Experiments of Dr. Wilson Philip, "Experimental Inquiry," &c., p. 56.

¶ By Remak, Müller's "Archiv," 1844, p. 463; Bidder, "Archiv f. Anat. und Physiol.," 1868, p. 1; Lee, "Philosophical Transactions," 1869; and Beale, "Quart. Journ. of Microscop. Sci.," April, 1869. See also Friedländer, "Unters. a. d. Physiol. Labor. in Wurzburg,"

have shown that whilst small ganglia and nerves are very generally distributed through the substance of the heart in the Frog, except near the apex of the ventricle, special collections of ganglia are found in two places: the first, known as the *ganglion of Remak*, is placed in the sinus venosus, near the opening of the inferior vena cava; the second, termed the *ganglion of Bidder*, is imbedded in the auriculo-ventricular septum. The functions of these ganglia may be demonstrated by experiment. If the heart of a frog after excision be kept thoroughly moist with blood or serum, it will continue to beat for many hours. The cause of the movement must necessarily therefore be in the heart itself, and may be in part attributed to a natural tendency of the cardiac muscular tissue to contract rhythmically and in part to the orderly discharge of impulses from nerve ganglia scattered through its substance. The stimulus to the ganglia of the excised heart is probably the contact of the blood or serum with the nerves of the endocardium, and the action of the heart is then said to be "automatic;" but when the heart is in position and acting naturally, the ganglia may be excited by stimuli applied to other parts of the body, and the heart is then said to be "reflectorially" excited. An experiment devised by Stannius* throws much light on the position and function of the cardiac ganglia. The two venæ cavæ (S.V.C., I.V.C., Fig 125) in this animal unite before entering the right auricle to form a dilatation called the sinus venosus (S.V.). The cavities of the right and left auricles, R.A., L.A., communicate with each other in consequence of the imperfection of the septum, but discharge their blood through separate orifices into the ventricle V., from which it is transmitted by a partially divided aorta (not shown in the Figure) to the lungs and brain, the lungs receiving chiefly the impure blood which has entered the ventricle from the right auricle, the head that which has been aërated from the left. In the wall of the sinus venosus is a ganglionic nerve mass termed the ganglion of Remak, and near the junction of the inter-auricular with the auriculo-ventricular furrow is a second one known under the name of Bidder's ganglion. Now, if a ligature be applied between the sinus venosus and the right auricle (at *a*) the heart suddenly ceases to beat, and remains in a state of relaxation or diastole, but the sinus itself continues to act. If the auricles or ventricle be directly stimulated, they immediately respond to the stimulus and execute a few movements. If a second ligature be applied between the auricles and ventricle, the auricles remain quiescent whilst the ventricle resumes its rhythmical action.

Fig. 125.



Diagrammatic representation of Frog's heart, to illustrate Stannius' experiments.

S.V.C., *I.V.C.*, Superior and inferior vena cava; *S.V.*, sinus venosus; *R.A.*, right auricle; *L.A.*, left auricle; *V.*, ventricle. The two ganglia are sufficiently indicated; *a*, position of one ligature; *b*, position of the other.

1867, and Schweigger-Seidel in Stricker's "Hum. and Comp. Histology," vol. i. 1878; Art. 'Heart,' p. 260.

* "Zwei Reihen physiologische Versuche," 1851.

224. The explanation advanced by Rosenthal of these phenomena is, that both the above-mentioned ganglia are automatic centres, receiving their stimulus to action within the heart. Remak's ganglion is extraordinarily irritable, the slightest stimulus conveyed to it being sufficient to cause it to liberate an impulse which, as its efferent fibres are distributed to both the auricles and the ventricles, induces their contraction. If a ligature be applied at *a* these efferent fibres are compressed or divided, and the heart is stopped in diastole. Bidder's ganglion is an accessory automatic ganglion that is much less irritable, requiring, for example, such a stimulus as the increased rush of blood to the heart that occurs in violent exertion to stimulate it. When the heart is arrested by the application of the ligature at *a*, the ventricle recommences its rhythmical action on the application of a ligature at *b*, because this acts as a powerful stimulus to the ganglion, and the auricle does not beat because the ligature happens to be above it; but if the ligature happens to pass through its centre, then both auricles and ventricle may be set in action. Another explanation suggested by Bidder is that Remak's ganglion is the proper automatic ganglion of the heart, receiving its stimuli from the endocardium, whilst Bidder's ganglion is excited to act reflectorially, that is to say, from stimuli acting on nerves outside the heart, which stimuli, after the application of the ligature, it no longer receives; or yet again, it may be that a ligature around the auriculo-ventricular furrow may stimulate the fibres of the vagus passing to a third ganglionic centre situated near the ganglion of Bidder, and possessing an inhibitory function. As long as Remak's ganglion and Bidder's ganglion act together they are superior to the inhibitory ganglion, and the heart continues to beat; but if the power of the inhibitory ganglion be greater than either of the two motor ganglia alone, when the connection between these two is severed the heart will remain at rest. The cardio-motor system of nerves may be affected by *mechanical*, *chemical*, *electric*, and *thermic* stimuli. Bernard, for example, observed acceleration of the heart's beats when the bulb of a thermometer, introduced through the superior vena cava, touched the endocardium; and a similar effect was noticed (in Mammals at least, though the opposite occurred in cold-blooded animals*) by Ludwig when the blood-pressure was increased. Again, the presence of blood or serum in the chambers of the heart greatly prolongs its activity, partly by its mechanical excitation, but partly also by affording nutritive materials and a supply of oxygen. The importance of oxygen is well shown by an experiment made by Wündt,† who observed that the heart of a frog continued to beat for twelve hours in oxygen, whilst it ceased to move in ordinary air after three hours, in nitrogen and hydrogen after one hour, and in vacuo in half an hour. Certain gases, as chlorine, sulphurous acid, hydrogen sulphide, and certain poisons, as strychnia, opium, Calabar bean,‡ are capable of more or less rapidly arresting the movements of the excised heart when directly applied to it, by their chemical action on the cardio-motor system. Various salts, as those of sodium and rubidium (Grandeau and Bernard) when in large quantity, and those of the biliary acids (Röhrig) slow or arrest the heart's action; as do also certain acids, as acetic and citric acid (Bobrik), and phosphoric acid (Leyden and Monk).

The action of induction shocks on the heart has been studied by Bowditch,§ Marey,‖ and Hildebrand,¶ and presents several points of interest. In the

* See Drosdow Hofmann's "Jahresbericht," Band iv. p. 37, "Phys. Theil."

† "Physiologie," 1873, p. 319. ‡ See Fraser, "Trans. Roy. Soc. Edinb.," vol. xxiv. p. 65.

§ Ludwig's "Arbeiten," 1872, Band vi. p. 139.

‖ Robin's "Journal d'Anatomie," 1877, p. 60.

¶ Abstract in Hofmann and Schwalbe's "Jahresbericht," Band vi. p. 53.

first place, each systole of the heart resembles a single vibration or *sécousse* of an ordinary voluntary muscle, differing only in the remarkably long interval that elapses between two successive *sécousses;* and whereas induction shocks applied to striated muscle cause the vibrations rapidly to fuse together, the muscle passing into a state of strong permanent contraction, named tetanus; in the case of the heart, the application of moderately strong and moderately frequently repeated shocks does not induce tetanus, but only accelerates the rhythmical contraction, and it is remarkable that a weak and a strong electrical stimulus alike cause the ventricles to contract with their maximum vigour. The vigour of each contraction depends in great measure on the interval between it and the preceding one.

Another peculiarity of the muscular tissue of the heart is that its excitability is not the same at all periods of a cardiac revolution; for although a very strong stimulus or shock will always induce a contraction, a weak shock will only cause contraction during a certain period of a complete revolution, the heart at another period being incapable of responding, or presenting what may be termed a "refractory phase," the duration of which varies with the intensity of the stimulus and the state of the heart. With weak stimulation the refractory phase of the ventricle lasts throughout the period of systole, with stronger stimulation it lasts only during the first part of the systole, and with strong currents disappears altogether. Heat abridges, cold protracts the refractory phase. The refractory phase of the auricles lasts during the greater part of the diastole of the ventricle. Upon the whole there is a strong tendency on the part of the heart to work uniformly, so that an artificially induced systole is followed by a longer diastole, whilst such a systole is always more vigorous and its latent period less in proportion to the interval that has elapsed since the last spontaneous systole. When a succession of weak electrical stimuli are made to act on the heart, the great majority find it in the refractory phase, and hence the number of systoles is much less than that of the irritations; but if the electrical shocks are made to increase in intensity, the refractory period becomes shorter and shorter, and the tracing rising by successive increments, so as to present a series of steps or "staircase beats," till at last, when the stimuli are sufficiently strong, the heart passes into tetanus. The action of *continuous currents* of short duration resembles that of induction currents, weak continuous currents of short duration applied during the non-refractory stage simply accelerating the beats, whilst strong currents send the heart into a state of tetanus. The rapidity with which the wave of contraction is propagated varies from 10–30 mm. ($\frac{1}{2}$–$1\frac{1}{4}$ inch) in a second,* or, according to Marchand, even to 0·1 mm. per second,† and the latent period amounts to from 0·115—0·221 sec. in summer frogs, and from 0·177—0·308 sec. in winter frogs.

225. *Effects of Variations of Temperature upon the Heart's Action.*‡—From

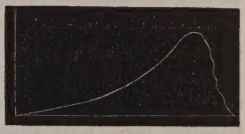
* Eugelmann, Pflüger's "Archiv," Band xi. p. 465.

† Marchand, Pflüger's "Archiv," Band xv. 1877, p. 511.

‡ The effects of variations of temperature upon the heart have been studied by Pickford, Henle and Pfeuff., "Zeits.," 1851; Calliburcés, "Gaz. Hebdomad.," 1857, p. 468; Tigger, "Dissert.," 1853; Liebermeister, "Deutsch. Archiv f. Klin. Med.," Band i. p. 464; Schelske, "Ueber der Veränderungen der Erregbarkeit durch die Wärme," Heidelberg, 1860; Panum, see Abstract in Schmidt's "Jahrbücher," 1858; Cyon, Ludwig's "Arbeiten," 1868, p. 77; and Brunton, "St. Bartholomew's Hosp. Reports," vol. vii. 1871, p. 216; Wernicke, Preyer's "Sammlung," Jena, 1876; Cleland, "Journ. of Anat. and Physiol.," vol. xi. p. 754; Prof. Garrod, "Proceed. Roy. Soc.," 1870, p. 351, 1875, p. 142, who is supported by Mr. Thurston, Humphrey's "Journal of Anatomy," vol. x. 1876, p. 501, finds that the length of the systole of the heart, as indicated in the radial artery, is constant for any given pulse-rate, and varies as the cube-root of the rapidity.

numerous experiments, chiefly made on the frog, it appears that the heart only beats within certain limits of temperature, though these are not very well defined; in regard to the lower limit of temperature, the hearts of some animals cease to beat at 32° F., others not till exposed to a temperature of 25° F.; in regard to the higher limit of temperature the variation is still greater, some hearts being arrested at 86° F., and others not till 104°. In ascending *slowly* from the lower to the higher limits, the frequency of the heart's action steadily increases till it reaches a maximum, and then as the higher limit is approached it suddenly, but somewhat irregularly falls, as is represented in the adjoining cut (Fig. 126), where the abscissa may be considered as divided into degrees of temperature, whilst the ordinates would represent the relative frequency of the heart's action. Near the higher limit at which the heart's movements are arrested, the heart beats irregularly, so that the duration of the successive periods of diastole vary considerably, and just before stopping the contraction of the heart is no longer sudden and complete, but undulatory or peristaltic in character. In regard to the variation in the force of the beats of the heart which occurs with rise of temperature, Cyon has shown that the curve representing it attains its maximum very near the lower limits of temperature, and remains at the same height till a temperature of between 59° F. and 66° F. is reached, from which it progressively falls to zero. At the higher temperature little or no fluid is propelled from the heart, owing to the peristaltic character of its contractions. The conclusion that may be drawn from the above facts is, that there is a certain temperature at which the combined frequency and force of the heart's action produces its greatest effect in driving the blood through the vessels. For the frog this lies, according to Cyon, between 64° and 72° F. The phenomena in Cyon's experiments were somewhat different when the changes of temperature in the air surrounding the excised heart, and the serum flowing through it were *sudden*. Cyon found that if a heart that had been beating regularly at about 70° F. were suddenly cooled to 32° F., the force of the contractions underwent great diminution, the movements assuming a peristaltic character, and the heart becoming considerably dilated (heat diastole). After a time, however, it began to beat more strongly, and behaved as if it had been gradually cooled. If after being kept at 32° F. for some time it was suddenly exposed to air and serum at a temperature of 104°, the beats succeeded one another more and more rapidly till the whole organ passed into a state of tetanus (heat tetanus), lasting from 15–30 seconds. It then began to beat again, and passed through the same stages in the course of 1½–2 minutes that it presented in being gradually warmed. When a heart was suddenly heated, not from 32° F., but from about 55° to 104° F., the beats instead of becoming quicker became slower and fuller, and the traces resembled those of a heart in which the vagus is irritated. This state lasted for 1–2 minutes, and then the heart passed through the same stages that it would otherwise have presented if it had been gradually warmed. It thus appears that if the temperature be raised above that of "heat diastole" "heat-rigor" is produced, and the movements of the heart cannot again be restored by cooling it. The excitability

Fig. 126.



Curve showing the increased rapidity of the heart's action as the temperature to which it is exposed rises.

Fig. 127.

Curves showing force of the contraction of the heart with increase of temperature.

of the inhibitory nerve apparatus is abolished during the arrest of the heart's action from heat, for Cyon has shown that irritation of the sinus venosus, which invariably produces arrest of the heart's action in diastole under normal conditions, causes tetanus of the ventricle when applied to a heart that is in a state of arrest from heat. In *warm-blooded animals* the frequency of the heart's beats also increases with the temperature within certain limits (Panum, Brunton). In one instance, by means of registering apparatus, Dr. Brunton found that the heart of a rabbit, when the animal was exposed to a temperature of 105° F., beat 472 times in a minute. After reaching a maximum the beats become slower, and the heart finally stops. The increase is not the same for each degree of rise in the temperature; and the number of beats at the same temperature, and also the amount of quickening for each degree of rise of temperature, differs in different animals. The upper limit at which the heart stands still in rabbits is about 113° or 114° F. (Brunton); as the temperature to which the heart is exposed rises, and the pulse quickens, the inhibitory power of the vagus diminishes, but when the temperature had risen in Dr. Brunton's experiments to nearly its upper limit, the power of the vagus was again observed to be increased, and—contrary to expectation—to be strongly marked just before the heart ceased to beat. Schiff* observed that stimulation of the vagus caused acceleration instead of slowing of the heart's movements in rabbits that had been kept for some time at a temperature of 37°–38° C. (98°–100° F.). It is not improbable that the increased frequency of the heart's action in febrile conditions of the system is in part due to the stimulating effect upon the heart of the increased temperature of the blood caused by augmented tissue change.

226. *Nerves Retarding or Inhibiting the Action of the Heart.*—In the year 1846 the brothers Weber† observed the important fact which proved the starting point of numerous researches on the influence of the nervous system upon the heart, that irritation of the Vagus, or of its inferior cut surface in the neck, by means of an interrupted current of electricity caused the rhythmical movements of the heart to become slower, and if the current were sufficiently

* Pflüger's "Archiv," 1878, p. 199.

† "Archiv d'Anat. Gén. et de Physiol.," Jan. 1846, and Wagner's "Handwörterbuch," Band ii. p. 31; see also Budge in "Archiv f. Phys. Heilk.," 1846, Band v. p. 319; v. Bezold, "Unters. üb. d. Innervat. des Herzens," 1863; Rutherford, 'Influence of the Vagus upon the Vascular System,' "Transact of Roy. Soc. Edinb.," vol. xxvi. 1870, p. 1 (in this paper references will be found to all the more important antecedent memoirs); Goltz, "Centralblatt," 1868, p. 593; Meyer, "Das Hemmungsnerven-system des Herzens," Berlin, 1869; abstract in "Journ. of Anat. and Physiol.," 1869, vol. iii. p. 445; Kowalewsky and Adamük, "Centralblatt," 1868, p. 546; Bernhardt, "Inaug. Dissert.," 8vo, p. 32, 1868; Aubert and Roever, "Centralblatt," 1868, p. 578; Coats, "Bericht d. k. Sachs. Gesell. d. Wissenschaft.," 1869; also the effects of irritation of the vagus on the internal work of the heart, "Leipziger Arbeiten," Band iv. 1870, p. 176; Michael Foster, 'Fullerian Lectures,' "Rev. des Cours Scientif.," 1869, Nos. 42, 43, and 45; P. Keuchel, 'Das Atropin, und die Hemmungsnerven,' "Inaug. Dissert.," 1868; Donders, "Centralblatt," 1870, p. 408; Masoin, "Bull de l'Acad. Roy. de Méd. de Belgique," t. vi. p. 4, 1872-3; Nuel, Pflüger's "Archiv," Band ix. p. 83; Boehm, "Studien über Herzgiften," 1871; Arloin et Tripier, "Archiv de Phys. Norm. et Path.," 1872, "Contribution à la Physiologie des Nerfs Vagues;" Schiff, "Herz- und Gefäss-nerven," abstract in "Centralblatt," 1873, Nos. 1, 2, 3; Metschnikoff and Setschenow, "Uber die Vaguswirkung auf. das Herz, Centralblatt," 1873, p. 163 and 289; Schiff, "Archiv f. Physiol. Heilk.," 8ter Jahr.; Moleschott, "Wien. Med. Wochens.," 25th May, 1861; and Lister, "Proceed. Roy. Soc.," vol. ix. p. 367, were led by their researches to consider the vagus as a motor nerve of extreme excitability, but which was easily exhausted. They maintained that with very feeble currents applied to it the heart's action is accelerated; but Pflüger, v. Bezold, Rutherford, Wündt, and many others have been unable to corroborate these statements. Later experiments have shown, however, that certain accelerator fibres do run in the trunk of the vagus; see Schiff's "Physiologie," 1859, p. 417 *et seq.*

strong arrested its movements altogether. Now in the case of any voluntary muscle the passage of such a current through the nerves supplying it produces either simple contraction, or if the shocks be sufficiently frequent, tetanus, but in the case of the heart the effect produced is, on the contrary, that of complete relaxation. The cessation of the rhythmical action in diastole is not, however, of long duration; contraction soon recommences, notwithstanding the continued application of the electrical stimulus, though it can be again arrested, or materially retarded, by passing the interrupted current through a fresh portion of the nerve situated lower down or nearer the heart. This recommencement of the heart's action is probably, as Rutherford first pointed out, the result of the accumulation of blood in the right cavities of the heart.* Comparative trials showed that a very much stronger stimulus is necessary so to excite the Cardio-inhibitory fibres of the Vagus that the heart's action may be arrested than is required to stimulate such a nerve as the recurrent laryngeal fibres, so that the laryngeal muscles may be thrown into action.† The woodcut (Fig. 129) will show by means of a tracing the effect of stimulation of the lower end of the Vagus in the rabbit. It will be observed that the undulations, each of which represents a cardiac contraction, are very rapid and small till the moment at which the stimulus is applied to the Vagus. They then become much slower, and larger, whilst their mean level falls, indicating a diminution of blood-pressure. As soon as the stimulus to the Vagus is withdrawn the contractions present their former frequency, and the blood-pressure again rises. Further inquiry by Cyon and Ludwig‡ soon showed that in the rabbit the Vagus gives off a branch immediately below the inferior laryngeal nerve, which may be called the Cardio-inhibitory of the Vagus (see Fig. 128), since, when excited, it is capable of exerting the same controlling, restraining,

Fig. 128.

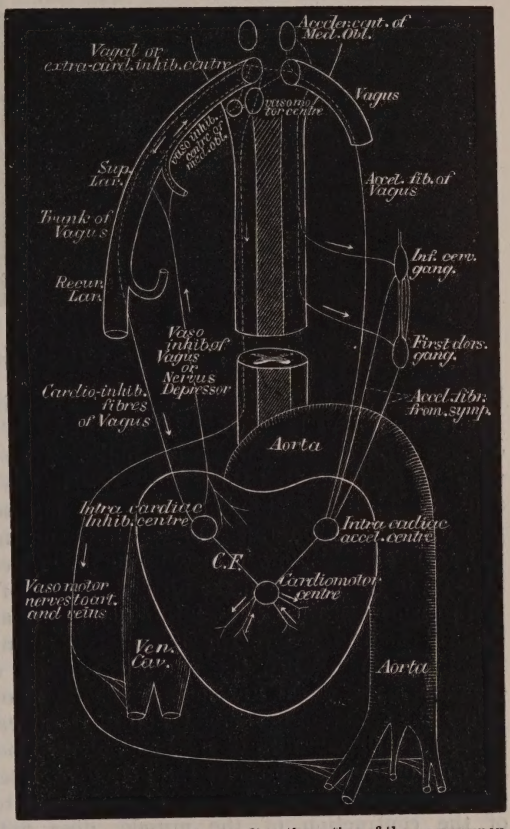


Diagram to aid in understanding the action of the nerves upon the Heart. The Right half represents the course of the inhibitory, and the Left the course of the accelerating nerves of the Heart; the arrows showing the direction in which impressions are conveyed. The ellipse at the upper extremity of the Vagus looking like the section of the nerve is intended to represent the Vagal nucleus or centre. In this diagram the nerves are incorrectly made to cross, instead of passing behind, the aorta.

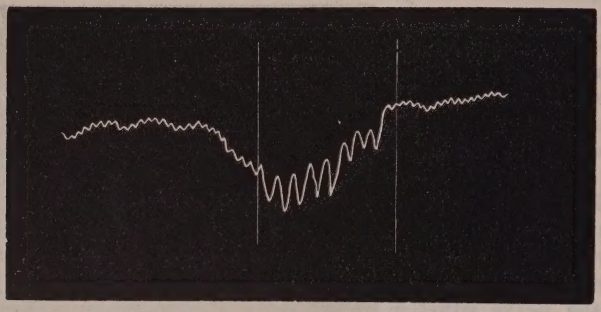
* "Journ. of Anat. and Physiol.," vol. iii. 1869, p. 410.

† Rutherford, 'On the Influence of the Vagus on the Vascular System,' "Trans. Roy. Soc. of Edinb.," vol. xxvi. 1870.

‡ Ludwig's "Arbeiten," 1867, p. 128.

arresting, or inhibitory power over the Cardiac movements as the Vagus itself. In man this nerve is represented by the superior Cardiac branch of the Vagus. If this nerve be divided on both sides and the upper cut surface of the nerve on either side be irritated no effects are produced, but if the lower cut surface

Fig. 129.



After. During. Before.

Tracing showing effect of stimulation of Vagus. The tracing must be read from right to left. The rise and fall of the tracing as a whole constitute the "respiratory curves."

be irritated, the heart stops in diastole. Slowing of the Cardiac beats occurs if only one Vagus be divided. The fibres of the nerve therefore appear to conduct impulses downwards (as indicated by the arrow in Fig. 128.). It might be supposed that these fibres pass to the Cardio-motor centre, and exert a direct inhibitory influence upon it, but several circumstances render it probable that an intermediate apparatus, or inhibitory mechanism which we may term an inhibitory centre, exists in the heart between the vagal branches running to the heart and the ultimate fibres of these branches. For, in the first place, when the Cardio-inhibitory nerves are stimulated a very appreciable interval elapses before the inhibitory action is manifested. Thus Pflüger found that even when the stimulus applied was strong enough to produce complete arrest of the Cardiac movements, two entire beats always intervened before the cessation occurred,* and in Donders' experiments, a period of 0·17 sec., or nearly one-fifth of a second, elapsed before arrest occurred. But in the case of ordinary muscles the period of latent excitation, or the time that elapses between the application of a stimulus to the nerve and the beginning of the contraction of the muscle, does not exceed 1–100 of a second. The long "latent period" seems to indicate that there are resistances to be overcome, and that the action of the stimulus is indirect. Secondly, Meyer† has been able by direct irritation of a particular part of the sinus venosus in the common eel by means of an interrupted current to arrest the heart's action for sixteen minutes, and in the frog he was occasionally able by persistent direct irritation to keep the heart at rest for an hour. Prof. Foster,‡ again, has pointed out that in certain Molluscs there is no nerve corresponding to the Vagus, but that the heart can be stopped in diastole by

* Pflüger found that the first perceptible effect of slight irritation of the Vagi is a prolongation of the diastole of the heart, or a retardation of the motor impulse, inducing the next contraction. When violent or long-continued excitation is applied to the Vagi, producing stoppage of the heart's action, the first beats on its recovery are usually very feeble; but when only moderately strong currents are applied, the first beats are often as energetic or even more powerful than before. This would seem to show that if the inhibitory influence is very strongly exerted it prevents the production of motor energy in the motor ganglia, whilst if it be moderately excited it does not interfere with its generation, but only with its discharge.

† "Das Hemmungsnerven-system," 1869.

‡ Pflüger's "Archiv f. Phys.," Band v. p. 191.

direct irritation when removed from the body. The inhibitory mechanism must in these instances be in the heart itself.

Evidence of an intermediate apparatus such as is represented in the above Figure as the intra-cardiac inhibitory centre is also derived from the action of certain poisons.* Thus Nicotin and Curare when injected subcutaneously in very small doses (1-8th to 1-3rd of a milligram) appear to stimulate the inhibitory centres, and the heart beats slower; but they soon paralyse these centres, and the heart then beats faster, and when this occurs irritation of the Vagus will no longer inhibit the heart's action, but if whilst the heart is beating faster Muscarin or Jaborandi be administered or the sinus venosus be irritated the heart still stops in diastole. The effects of Atropin are remarkable, for if a small quantity be injected subcutaneously the heart immediately begins to beat more rapidly, but its condition so far differs from its increased action under Nicotin that it can no longer be stopped in diastole by irritation of the sinus venosus, or the administration of Muscarin. The explanation of this appears to be that whilst Nicotin and Curare in certain doses and stages of their action paralyse the vagal centre, and the cardio-inhibitory fibres of the Vagus, so that these can no longer transmit inhibitory impulses, they do not paralyse the Intra-cardiac inhibitory centres, as is indicated by the effect of direct irritation on the sinus venosus. Atropin,† on the other hand, not only paralyses the vagal inhibitory centre, but it also paralyses the intra-cardiac inhibitory centres, for the heart under its influence is no longer capable of being arrested in diastole, either by irritation of the vagus or of the sinus venosus.‡ Dr. Brunton is disposed to think that Atropin acts especially on the connecting filaments, C F, between the inhibitory and cardio-motor centres.§ Continued stimulation of one Vagus annuls or prejudices the inhibitory action of the other.‖ In the course of an elaborate series of experiments upon the action of the nerves on the heart, v. Bezold observed that in animals under the influence of Curare, in which therefore all muscular movements that might complicate the phenomena were prevented, on applying electrical excitation to the upper cut surface of the divided Vagus, the blood-pressure fell, and he also observed that similar irritation applied to the medulla oblongata caused considerable elevation of blood-pressure, which still occurred, even when the two Vagi had been divided. He concluded that the spinal cord contained fibres acting directly on the heart. He further noticed that on division of the spinal cord in the cervical region the blood-pressure immediately fell, whilst if the posterior cut surface of the cord was irritated the blood-pressure again rose. Ludwig and Thiry on repeating v. Bezold's experiments substantiated their accuracy, and noticed that even when all the fibres passing from the spinal cord to the heart were destroyed by means of a galvano-caustic wire, the effects observed by v. Bezold to result from irritation of the cord could still be manifested. They concluded that the rise in the blood-pressure and augmentation in the frequency of the beats of the heart, were due to the constriction of the small vessels in the body generally, and in this conclusion they were supported by the results of ligatures applied to the aorta or larger arteries. Further investigations, the details of which were published in Ludwig's "Arbeiten" in

* See the papers of Truhart, 'Inaug. Dissert.,' "Beiträg. zur Nicotin-Wirkung, Dorpat," 1869; and Schmiedeberg, Ludwig's "Arbeiten," Band v. 1871, p. 41.

† If, however, Curare be given in excess of a certain dose, stimulation of the Vagus causes acceleration of the pulse. See Böhm, "Archiv f. Experiment. Pathol.," Band iv. p. 351.

‡ The effect of the administration of Atropin in man is to raise the number of the pulse from 72–80 to 140–180 in the minute. § "Brit. Med. Journ.," Dec. 16th, 1871, p. 689.

‖ Gamgee and Priestley, Foster's "Journ. of Physiology," vol. i. p. 40.

1866, enabled them to announce their discovery of the functions of a small nerve given off from the vagus, and to which they applied the name of *Nervus Depressor*. This nerve arises in the rabbit from the vagus, immediately below the superior laryngeal nerve, from which it often receives a reinforcing filament; and descending through the neck it is distributed to the heart. If this nerve be divided and the lower cut surface be stimulated, no effects are observed; but if the upper cut surface be irritated, an inhibitory action on the heart, together with a marked diminution of pressure in the whole arterial system, immediately becomes manifest, and the animal gives indications of pain. The direction in which it conducts impulses is therefore exactly the opposite to that of the cardio-inhibitory nerve of the Vagus—it is an afferent nerve. If the application of the stimulus be continued, the slight slowing action on the heart passes off, but the blood-pressure continues to fall till it only reaches two-thirds or one-half of its ordinary amount. The fall of the blood-pressure in the above experiment is small if the splanchnic nerves be divided before the application of the stimulus to the depressor nerve. The explanation of these phenomena seems to be that when a stimulus is first applied to the depressor nerve, an impulse is conducted to the vagal centres, from whence an inhibitory influence is directed through the cardio-inhibitory nerves to the intra-cardiac inhibitory centre, and the heart is slowed; but the depressor nerve also contains fibres which exert a restraining or inhibitory power over a vaso-motor centre in the medulla oblongata. Under ordinary conditions a nervous influence is discharged from the vaso-motor centre by fibres which, descending along the spinal cord, emerge with the several roots of the spinal nerves, enter the splanchnics, and are distributed to the smaller vessels throughout the body (one only being shown in Fig. 128). This nervous influence maintains the vessels in a state of permanent tonic contraction, which keeps up the blood-pressure to its normal height. But when the *depressor nerve* is stimulated, an impulse is conveyed to a vaso-inhibitory centre of the medulla oblongata, which re-acting on the vaso-motor centre inhibits its action, and the downward current from this through the spinal cord being consequently arrested, the great system of abdominal vessels dilates and the blood-pressure sinks. The result of this again is that the medulla receives less blood, the vagal inhibitory centres consequently become less active, whilst the heart resumes its ordinary activity. If, however, the splanchnics be first divided the arterial pressure is already greatly reduced in consequence of the extreme dilatation of the abdominal vessels, and the stimulation of the depressor nerve necessarily fails to exert any influence upon them; the blood-pressure therefore remains unchanged. It has been pointed out by Dr. Rutherford, that the inhibitory fibres of the vagus may be excited to action by stimulation applied to: 1. The central end of the vaso-inhibitory or superior cardiac branch of the vagus (depressor nerve); 2. The central end of the vagus of the opposite side; 3. Almost any sensory nerve in the case of warm-blooded animals, the fifth (according to Hering and Kratschner) having a very special action; 4. The abdominal viscera in the frog; 5. The splanchnic and cervical sympathetic. In these instances the cardio-inhibitory nerves appear to be excited in a reflex manner. The inhibitory action of the *right* Vagus upon the heart is much more marked than the left in the tortoise.* It may just be noticed that both Dr. Rutherford and Dr.

* Meyer (Op. cit.). In pigeons and rabbits Masoin (Op. cit.) and Arloing and Tripier (Op. cit.) state that of the left is greatest. Though coursing in the trunk of the vagus, the inhibitory nerves seem really to be derived from the spinal accessory, since if the fibres of the spinal accessory which Bernard has shown spring from the medulla oblongata and join

Coates,* of Glasgow, have shown that irritation of the vagus always diminishes the absolute amount of work done by the heart. A difference exists between the action of the vagi on the heart in the Frog and in mammals. If in the Frog one vagus be stimulated till it is exhausted and the heart begins to act again, stimulation of the other vagus causes prolongation of the diastole. But in mammals under the same circumstances, when the stimulus is applied to the second vagus, the heart instantly *pulsates*. This has been termed the "interference action" of the vagi.† Schiff‡ finds that if the heart be made to work with a ·6 per cent. solution of common salt or phosphate of soda, the inhibitory action of the vagus is lost, but returns when blood is readmitted.

227. There is reason to believe that the depressing effects of *shock* may be exerted both through the vagus and through the sympathetic system of nerves, and that considerable disturbance may ensue from lesions of such branches of these nerves as are most nearly connected with the heart. For the well-known fact of sudden death not unfrequently resulting from a blow on the epigastric region, especially after a full meal, without any perceptible lesion of the viscera, seems to indicate that a violent impression upon the widely-spread cœliac plexus of Sympathetic nerves (which will be much more extensively communicated to them when the stomach is full, than when it is empty), may cause the immediate cessation of the heart's action probably by a reflex action conducted to the cord and reflected through the pneumogastrics to the heart, in the same manner as a severe injury of the brain or spinal cord. This effect is not observed if the two vagi or the medulla be divided. A case has been put on record, in which the heart's pulsations were occasionally checked for an interval of from 4 to 6 beats, its cessation of action giving rise to the most fearful sensations of anxiety, and to acute pain passing up to the head from both sides of the chest—these symptoms being connected, as appeared on a post-mortem examination, with the pressure of an enlarged bronchial gland upon the great cardiac nerve.§ Czermak‖ has produced all the usual effects of irritation of the vagus in his own person by carefully-applied pressure over the vagus in the neck.

228. *Nerves Accelerating the Action of the Heart.*—The action of the heart cannot only be rendered slower or stopped by irritation of certain fibres running in the vagus, but by the irritation of other nerves its movements can be accelerated. V. Bezold observed that irritation of the cervical sympathetic is followed by increased frequency of the heart's beats, but that this effect is not constant.¶ Much more marked increase follows irritation of the communicating filaments running between the spinal cord and the inferior cervical and first dorsal ganglia of the sympathetic. Irritation of the spinal cord

the vagus, be torn out, it will be found impossible to arrest the heart's action by irritation of the vagus trunk, even as early as three days after the operation, that is, before degeneration of the nerve's fibres could have set in (Brücke, "Vorlesungen," 1874, Band ii. p. 94), though it can be immediately produced by irritation of the opposite vagus.

* Ludwig's "Arbeiten," 1869.

† Tarchanoff, "Trav. du Lab. d. Marey," 1876, p. 289; see also Meyer, "Jahresber.," Band vi. p. 58.

‡ "Jahresber.," 1877, Band vi. p. 58.

§ Müller's "Archiv," 1841, Heft 3; and "Brit. and For. Med. Rev.," Oct. 1841.—It may be surmised that in many cases of *angina pectoris*, in which no lesion adequate to account for death could be discovered, some affection of the cardiac plexus might have been traced on more careful examination.

‖ "Jenaische Zeits.," 1865, p. 384.

¶ See the researches and experiments of A. v. Bezold, "Untersuchungen über die Innervation d. Herz.," Leipzig, 1863; Ludwig and Thiry, "Sitz. d. k. Akad. zu Berlin," Band xlix.; Cyon, "Sitz. d. k. Sachs.-Gesell. d. Wiss.," 1866, and "Comptes Rendus," 1867, pp. 670 and 1049; Karl Bever, "Würzburg Medicin. Zeitsch.," Band vii. p. 215; Rutherford, "Transact. Roy. Soc. Edin.," 1870, vol. xxvi. p. 1, and his excellent Lectures in the "Lancet," in 1871–72.

itself, and of the medulla oblongata, causes increased frequency of the pulse, though this has been shown by Ludwig and Thiry to be a complicated phenomenon, and due in part to the effect of such irritation in producing contraction of the smaller arteries. The accelerating fibres, however, seemed from their observations to arise from centres in the medulla oblongata and spinal cord,* and emerging from the latter by the rami communicantes to enter the sympathetic ganglia, and to proceed from thence to the heart (see Fig. 128, right side). This view is supported by the experiments of v. Bezold and the brothers Cyon,† who have eliminated the influence of vascular innervation by division of the spinal cord between the first and second dorsal vertebra. The vessels are then permanently paralysed; but irritation of the spinal cord in the cervical region will still be found to produce considerable increase in the frequency of the pulse, though the variations of blood-pressure are slight or nil. Cyon believes that two accelerating branches are given off from the first thoracic ganglion. The course of the accelerating fibres has been much elucidated by the careful dissections of Schmiedeberg‡ made upon the dog. In this animal the vagus and sympathetic run together as far as the inferior cervical ganglion. Here they separate, and the vagus then gives off the recurrent laryngeal. The last cervical and first dorsal ganglion of the sympathetic are connected by two filaments, the upper one of which often joins the vagus. The inferior cervical ganglion gives off the superior cardiac nerve, and sometimes the inferior cardiac, though both not unfrequently come off from the vagus. One of them is sometimes absent, and both appear to act as accelerators (though they sometimes contain inhibitory fibres) and to reach the sympathetic through the roots connecting the sympathetic with the cord. In the Rabbit, the fibres directly accelerating the action of the heart proceed from the medulla oblongata, or possibly from the brain, and descending through the cervical portion of the cord, emerge as in the dog, opposite the inferior cervical and first dorsal ganglion of the sympathetic which they enter, and then proceed to the heart. In the Cat the accelerating fibres run chiefly in the right vagus.§ Stricker and Wagner‖ maintain that they descend from the medulla oblongata through the spinal cord as low as to the sixth dorsal vertebra, and that they pass out by the *rami communicantes* which connect the dorsal nerves with the sympathetic trunk. They then traverse the *ganglion stellatum* or first thoracic ganglion, and enter the Ansa Vieusenii, from whence they pass to the heart. Hence section of the rami communicantes or of the Ansa Vieusenii slows the heart. Schiff¶ denies the existence of accelerator nerves either in the cervical portion of the spinal cord or in the sympathetic. He derives them from the spinal accessory nerve, and believes that they run chiefly in the right vagus. He has not observed any retardation of the heart's action after section of the rami communicantes or of the Ansa Vieusenii. In the Frog the vagus contains accelerating as well as inhibitory fibres, for Wündt** has shown that, at a certain stage of poisoning with Curare, irritation of the vagus no longer causes slowing but quickening of the heart's action; and the same has been noticed in the action of Atropin and Nicotin. On grounds similar to those

* And one may possibly be situated even in the brain, since a larger region of the cerebral surface causes, when stimulated, increased frequency of the pulse. Schiff, "Jahresber. f. Anat. u. Physiol.," Band iii. Abth. iii. p. 31.

† "Archiv f. Anat. and Physiol.," 1867. ‡ Ludwig's "Arbeiten," Band vi. 1871, p. 34.

§ Nüssbaum, "Beiträge zur Anat. u. Physiol. der Herznerven," Dorpat, 1875; and Böhm, "Archiv f. Experim. Pathol.," Band iv. pp. 255 and 351.

‖ "Wien Acad. Sitzungsber.," Band lxxvii.

¶ "Centralblatt," 1873, Nos. 1, 2 and 3; and Pflüger's "Archiv," Band xviii. p. 202.

** "Verhand. des Naturhist.—Med. Ver. zu Heidelberg," 1859.

which have led to the admission of an intra-cardiac inhibitory centre, the existence of an intra-cardiac accelerator centre, or series of centres, seems probable. The accelerating fibres appear to be less easily excited and less readily exhausted than the inhibitory fibres.* They render the contractions of the heart more sudden as well as more frequent but less powerful.† The latent period is very long, amounting even to 10 seconds. Schiff finds that if the blood of frogs be replaced with a saline solution in Cyon's method the inhibitory power of the vagus is abolished, whilst its accelerating is retained.‡ Baxt§ has investigated the influence of the duration of the stimulus in cases of maximum stimuli. The duration of the application of the current lasted from 1 to 36 seconds, and in all instances the vagi were divided and the animals moderately curarized. The absolute number of beats induced by maximum stimuli was almost entirely independent of the duration of the stimulus, and of the previous and very varying rapidity of the action of the heart, whilst it was remarkably constant in the same animal. Further, the rapidity with which the maximum frequency of beat is attained is independent of the duration of the stimulus. Thus, after the application of a stimulus lasting only 1 second, the heart attains its maximum frequency of action in from 8-10 seconds, which is quite as rapidly as when the stimulus is applied for a longer period, but the effect lasts a much shorter time.

229. During the last few years the action of numerous poisons on the heart has been made a subject of special investigation, but the results at present obtained scarcely admit of being accurately classified. Some appear to act as paralysers, others as excitors of the motor and inhibitory nerves respectively; others, as the sulphocyanide of potassium,‖ act directly on the muscular tissue, rendering it incapable of responding to the strongest stimuli. And others, again, indirectly influence the force and frequency of the heart's action by their action on the respiratory, or upon the vaso-motor systems of nerves. When it is remembered that different animals are not affected in the same manner by particular poisons, and that there is frequently a difference between the effects of large and small doses, it may be conceived that the difficulty of explaining the phenomena observed is extreme. It may be observed, however,¶ that some poisons, as the Antiaris toxicaria;** Tanghinia venenifera;†† Digitalis; Helleborus niger; Helleborus viridis; the green resin obtained from the Nerium oleander;‡‡ Squill; Manganja, from the Zambesi river (Dr. Sharpey); and Carroval and Vao, from the river Darien;§§ most of which have been examined by Drs. Fagge and Stevenson, produce in frogs a peculiar form of irregularity in the action of the heart, attended with protrusion of its walls at different points, and acceleration of its beat; then diminished frequency, caused by protraction of the ventricular systole;

* And in support of this Mitchell and Morehouse ("Smithsonian Contribution to Knowledge," Washington, 1863, p. 37) state that in Chelonians whilst galvanization of the vagus arrests the heart's movement, gentle irritation causes the heart to beat more rapidly.

† Badoud, "Verhand. d. Phys. Med. Gesellsch. zu Würzburg," N. F., Band viii. p. 12.

‡ Pflüger's "Archiv," Band xviii. p. 203. § "Archiv f. Anat. u. Phys.," 1877, p. 521.

‖ C. Bernard, "Leçons sur les Substances Toxiques, &c.," 1857, p. 358; MM. Ollivier and Bergeron in Brown-Séquard's "Journal de la Physiol.," 1863, pp. 35 and 47; and MM. Dubreuil and Legros, "Comptes Rendus," 1867, p. 1256.

¶ See T. R. Fraser, M.D., 'On the Physiological Action of the Calabar Bean, Physostigma venenosum,' from the "Transact. of the Roy. Soc. of Edinb.," vol. xxiv. 1867, and the paper 'On the Application of Physiological Tests for certain Organic Poisons, and especially Digitalin,' by Dr. Fagge and Dr. Stevenson, in "Guy's Hosp. Rep.," 1846, p. 47.

** Neufeld, "Stud. des Physiol. Instit. zu Breslau," 1865, Heft 3.

†† Pelikan and Dybkowski, "C. Rend.," 1856, p. 1209. ‡‡ Pelikan, ibid., 1866, p. 237.

§§ Hammond, "Amer. Journ. of Med. Sci.," 1859, July, p. 13.

and, finally, stoppage of the contractions by cessation of the dilatation of the ventricles, which remain contracted, white, and perfectly empty. The stoppage usually occurs in from five to twenty minutes after the administration of the poisonous dose, and the animal retains its control over the voluntary movements for a quarter of an hour or more after the heart has ceased to beat. Calabar bean, on the other hand, according to Dr. Fraser, is a poison that produces cardiac paralysis in an exactly reverse manner. It causes no acceleration, but exciting the vagal centres it diminishes the frequency of the contractions by prolonging the ventricular diastole; and it produces the final stoppage by cessation of the contraction of the ventricles, which then remain dilated, dark, and full of blood.* The Atropin group of bases—viz., atropin, hyos-

* Arsenious acid (Cunze, "Zeits. f. Rat. Med.," Band xxviii. p. 33, and Sklarek, Reichert's "Archiv," 1866, p. 481), bromide of potassium (Eulenberg and Guttmann, "Compt. Rend.," 1867, p. 1281), the salts of barium and of oxalic acid (Cyon, Reichert's "Archiv," 1866, p. 196), chloroform (P. Q. Brondgeest, "Nederland. Arch.," 1865, p. 473, and Dogiel, Reichert's "Archiv," 1866, pp. 231 and 415), nicotin, quinine (Eulenberg, "Compt. Rend.," 1867, p. 421, Solyet, ibid. 1867, p. 719), strychnia (Heineman, Virchow's "Archiv," xxxiii. p. 394), the arrow poison of Borneo (Braidwood, "Edin. Med. Journ.," Aug. 1864), aconitina (Achscharumow, Reichert's "Archiv," 1866, p. 281), caffein and thein (Leven, in "Archives de Physiologie," 1868, p. 481), delphinin (Böhm, "Centralblatt," 1871, p. 586), muscarin (Schmiedeberg, Ludwig's "Arbeiten," Band v. 1871, p. 41, and Band vi. 1872, p. 34), and the gases sulphuretted hydrogen (Kaufmann and Rosenthal, Reichert's "Archiv," 1865, Heft 6), hydrocyanic acid (Preyer, "Archiv f. Path. Anat.," Band xl. p. 125), carbonic oxide (Pokrowsky, ibid. 1866, Heft 1, and Traube, "Cbl.," No. 10, 1866), carbonic acid (Cyon, "Compt. Rend.," 1867, p. 1049), or blood saturated with them, seem all to exercise a depressing influence upon the motor ganglia of the heart, causing it to stop in diastole, in some instances (aconitina) with, in other (delphinin) without, a preliminary stage of accelerated frequency of beat and augmented blood-pressure. When the stoppage in diastole is sudden, as occurs when blood charged with carbonic acid is transmitted through the heart, the effect may with probability be referred to direct stimulation of the extremities of the pneumogastric or inhibitory nerves. Cinchonin accelerates the action of the heart (Elson, "Amer. Journ. of Med. Science," 1866, July, p. 9). Atropin (v. Bezold and Blöbaum, "Unters. aus der Physiol. Labor. zu Würzburg," 1867, p. 1) paralyses the terminal branches of the vagus in the heart. The feeble influence exerted by the vagus over the cardiac movements in rabbits explains in part their immunity from the injurious effects of large doses of the poison (see Dr. Ogle, "Med. Times and Gaz.," 1867, p. 466). For other papers on the action of poisons on the heart, see Boehm ("Studien üb. Herzgifte," Pamphlet, and Abstract in "Centralblatt," 1871, p. 584), Basch and Oser ('Wirkungen des Nicotins,' "Wien. Med. Jährb.," 1872, p. 367), Polaillon et Carville ("Les Effets Toxiques de l'Inée, Poisons de Pahoions"), Gabor ("Archiv d. Physiol.," 1872, pp. 523 and 680), Ackermann ('Wirkungen des Digitalins,' "Deutsche Archiv f. Klin. Med." 1872, Band xi. 125), and Volkmann's "Sammlung Klin. Vorträge," No. 48; Brunton ("On Digitalis," 1868), Fothergill ("Digitalis" 1871), Oulmont and Laurent ('On Hyoscyamin and Daturia,' "Archiv. de Physiol.," Nos. 2 and 3, 1870), Holmes ('On Ergot,' "Arch. de Phys.," 1870, p. 384), Fick ('Die Wirkung des Sparteins,' "Archiv f. Experiment Path.," Band i. 1873, p. 397), Nunneley ("Proc. Roy. Soc.," June, 1869, and "Practitioner," 1869, p. 347, action of atropin, digitalin, aconitin, strychnia, veratria, morphia, nicotin, conium, and bromide of potassium), Arnstein and Sustschinsky, 'Ueber die Wirkung des Calabar auf die Herznerven,' in "Würzburg Phys. Untersuch.," Band iii.), Buchheim and Loos ("Neb. die Pharm. Gruppe des Curarins," Pamphlet), Wood, 'Viridia and Veratroidia,' "Amer. Journ. of Med. Sci.," 1870), Weyland ("Vergleich Unters. über Veratrin, Sabadillin, Delphin, Emetin, Aconitin, Sanguinarin and Chlorkalin), Blake ('Action of Inorganic Substances when introduced directly into the Blood,' "Journ. of Anat. and Physiol.," 1870 and 1873), and many others. Much discussion has arisen in regard to the question whether the inhibitory power of the pneumogastric nerves upon the heart is affected by the administration of curare, Bernard ("Leçons sur les Effets des Substances Toxiques," 1857, pp. 348, 352, 373), Kölliker (Virchow's "Archiv," Band x. 11, 17, 39, 73, and "Med. Central Zeitung," 1858, No. 58), Heidenhain ("Allg. Med. Central Zeit.," 1858, No. 64), Funke ("Lehrbuch," 4th edit. 1863, pp. 959 and 979), Goltz (Virchow's "Archiv," Band xxvi. p. 24), and Budge ("Physiologie," 1862, p. 549), considering it to be proved that these nerves are rendered incapable of transmitting their inhibitory influence; whilst v. Bezold ("Central. Zeit.," 1858, Nos. 49 and 59), Vulpian ("Gaz. Méd. de Paris," 1858, No. 27, p. 429), Meissner ("Zeits. f. Rat. Med.," 3 R., Band vi. p. 506), Bidder (Reichert's

cyamin (which is an atropin containing 1 eq. of methyl ammonium instead of 1 eq. of hydrogen), conium, daturin, together with physostigmin, aconitin, delphinin, and veratrin first, or in small doses, stimulate, and then *lower* or *abolish* the excitability of the inhibitory centres.* The intra-cardiac inhibitory centres are stimulated by muscarin, and with suitable arrangements to prevent desiccation the heart of a frog may be kept motionless in diastole for hours under its influence, but if it be acted upon by a solution of atropin it soon again resumes its ordinary movements. Referring to Fig. 128, it may be said that the cardio-inhibitory fibres of the vagus are excited by nicotin and paralysed by curare, that the intra-cardiac inhibitory centre is excited by muscarin, and that the connecting filaments, C, F, between the intra-cardiac inhibitory and motor centres are paralysed by atropin and excited by Calabar bean.

230. There seems adequate reason to believe that the whole, or very nearly the whole, of the blood contained in the Ventricles is discharged from them at each systole; for the left ventricle is very frequently found quite empty after death; and if a transverse section be made through the heart, when in a state of well-marked *rigor mortis* (which may be considered as representing its ordinary state of complete contraction), the ventricular cavity is found to be entirely obliterated.† The total quantity discharged from either ventricle of the Human heart at each systole is estimated by Valentin at 5·3 oz., by Volkmann at 6·2 oz., and by Vierordt at 6·3 oz.; but these amounts are deduced from calculation of the (supposed) total of the blood, divided by the estimated duration of its passage through the heart, rather than from actual admeasurement. The time occupied by the Blood in making an entire circuit of the body was attempted to be ascertained by Hering,‡ by introducing prussiate of potash into one part of the system, and drawing blood from another. He states that he detected this salt in blood drawn from one of the jugular veins of the Horse in about 30 seconds after it had been introduced into the other; in which brief space the blood must have been received by the heart, have been transmitted through the lungs, have returned to the heart again, have been sent through the carotid artery, and have traversed its capillaries. These experiments have been fully confirmed by those of Poiseuille,§ and of Mr. Blake,‖ who found that a solution of nitrate of baryta injected into the jugular vein of a Horse appeared in the blood of the carotid artery of the opposite side after an interval of 15 seconds. The same inquiry has been pursued, with improved means, by Vierordt.¶ This observer affixed a number of small cups to a drum which was made to rotate at a certain velocity in front of the opened vein; analyses of the contents of the several vessels enabled him to ascertain with great accuracy the moment at which the salt injected made its appearance. In this way he determined the number of seconds occupied by the blood in performing one entire revolution to be, in Squirrels 4·39, in Cats 6·69, in the Hedgehog 7·61, in Rabbits 7·79, in the Dog 16·7, in the Horse 31·5, in the Cock 5·17, in the Duck 10·64, and in the

"Archiv," 1865, No. 3, p. 337), contend that this agent does not paralyse the vagi, no loss of regulatory or inhibitory power being observable between poisoned and healthy animals. Bidder arrived at the latter conclusion in reference to the splanchnic nerves, and their influence upon the intestines. He noticed also, in opposition to Kölliker, that in poisoning by curare great dilatation of the pupil, indicating the persistence of the agency of the sympathetic, occurred, and he perceived no indications of paralysis of the vaso-motor nerves. This contradictory testimony is probably referrible to differences in the composition of the poison and in the quantity administered.

* See Rossbach, "Verhand. d. Med., Verhand. zu Würzburg," and Boehm, op. cit.

† Kirkes' "Handbook of Physiology," 2nd edit. p. 80.

‡ Tiedemann's "Zeitschrift," vol. iii. p. 85.

§ "Annal. des Sciences Nat.," 1843, Zool. t. xix. p. 32.

‖ "Edin. Med. and Surg. Journ.," Oct. 1841. ¶ "Phys. d. Mensch.," 1861, p. 111.

Goose 10·86. He estimates the period in Man at 23·1 seconds (during which there are 28 beats of the heart), of which 2 seconds at most are occupied in traversing the larger arteries, 2½ to 3 seconds in passing through the smaller arteries, 3 seconds for the capillaries, and 4 or 5 seconds for the venous system, which numbers must be multiplied by two for the two circulations. Moreover, the coincidence between the cessation of the heart's action, and the diffusion of the salt through the arterial blood, bears a striking correspondence; and it may be hence inferred that the arrestment of its muscular movement is due to the effect of this agent upon its tissue, when immediately operating upon it, through the capillaries of the coronary artery.—This conclusion is borne out by a variety of other experiments, which show that the time of the agency of other poisons that suddenly check the heart's action (which is the special property of *mineral* poisons), nearly coincides, in different animals, with that which is required to convey them into the arterial capillaries. And it seems to derive full confirmation from the fact, that poisons which act locally on other parts give the first indications of their operation in the same period after they have been introduced into the venous circulation. Thus, in the Horse, the time that is required for the blood to pass from the jugular vein into the capillary terminations of the coronary arteries is 16 seconds, as is shown by the power of nitrate of potash to arrest the heart's action within that time; and nitrate of strychnia, injected into a vein, gave the first manifestation of its action on the Spinal Cord in precisely the same number of seconds. In the Dog, the heart's action was arrested by the nitrate of potash in 11 or 12 seconds; and the tetanic convulsions occasioned by strychnia also commenced in 12 seconds. In the Fowl, the former period was 6 seconds, and the latter 6½; in the Rabbit, the first was 4, and the other 4½ seconds.—From such experiments it seems evident that the rapidity of the circulation is underrated, in any estimate that is founded upon the capacity of the Heart, and its number of pulsations in a given time; and it is difficult to see how the two sets of facts are to be reconciled. According to Hering, the rapidity of the circulation diminishes with age; and Vierordt has shown that with increased frequency of the heart's action there is in general an increased rapidity of the circulation, at least in the higher Vertebrata. Still it by no means follows that an increase in the frequency of the heart's action in a particular animal should be always accompanied by an increased rapidity in the current of the circulation; in point of fact, the experiments of Hering* show that, in the Dog and Horse, when inflammatory or febrile conditions, such as Pericarditis, are set up, a much longer period is occupied in the passage of the blood than before.

231. The *number* of contractions of the Heart in a given time is liable to great variation, within the limits of ordinary health, from several causes; the chief of these are diversities of Age, of Sex, of Stature, of Muscular exertion, of the activity of the Respiratory process, of the condition of the Mind, of the state of the Digestive system, and of the Period of the day.

a. Putting aside the other causes of uncertainty, the following Table may be regarded as an approximation to the average frequency of the Pulse, at the several *Ages* specified in it, taking equal numbers of Males and Females.

	BEATS PER MINUTE.		BEATS PER MINUTE.
In the fœtus in utero	140—150	From the 7th to the 14th year .	80—90
Newly-born infant	130—140	From the 14th to the 21st year .	75—85
During the 1st year	115—130	From the 21st to the 60th year .	70—75
During the 2nd year	100—115	Old age†	75—80
During the 3rd year	95—105		

* "Archiv f. Phys. Heilk.," 1853, t. xii. p. 133.

† The rise in the average frequency of the pulse in very advanced life, contrary to the

b. The difference caused by *Sex* appears from the inquiries of Dr. Guy,* to be such, that the pulse of the adult Female is more frequent than the pulse of the adult Male, at the same mean age, by from 10 to 14 beats in a minute.

c. The influence of *Stature* is affirmed by Volkmann to be tolerably well defined. The pulse being *cæteris paribus* less frequent as the stature is greater; so that if the pulse of a man of $5\frac{1}{2}$ feet high were 70 per minute, that of a man of 6 feet would be 66·7, and that of a man of 5 feet, 73·8.

d. The effect of *Muscular Exertion* in raising the pulse is well known; as is also the fact, which is one exemplification of it, that the pulse varies considerably with the *posture* of the body. The amount of this variation has been made the subject of extensive inquiry by Dr. Guy; and the following are his results:—In 100 healthy Males, of the mean age of 27 years, in a state of rest, the difference between standing and sitting was 10 beats, or about 1–8th of the whole number of beats per minute; the difference between sitting and lying was 5 beats, or 1–13th of the whole; and the difference between standing and lying was 15 beats, or 1–5th of the whole. In 50 healthy Females of the same mean age, the difference between standing and sitting was 7 beats, or 1–13th of the whole; that between sitting and lying was 4, or 1–24th of the whole; and that between standing and lying was 11, or 1–8th of the whole. Dr. Ed. Smith has made similar and very extended observations on Adults in Phthisis and on Children in health; and conjoined with them the influence of period of the day. He found in Phthisis, at 8 A.M., the increase, on assuming the sitting and standing postures, was in each case 10 pulsations per minute, but at 4 P.M. it was reduced to 7, and on the whole average there was an increase of $8\frac{1}{2}$ pulsations in each posture. In healthy Children, at 8 A.M., 12 (noon), 5 P.M., and 8 P.M., the increase in the sitting posture was 1 2 : 9 : 7·3 : 3·5 pulsations, whilst in the standing posture it was 27 : 14·6 : 12 : 10 pulsations per minute: results which seemed to show that the irritability of the heart, augmented by the rest and quiescence of sleep, undergoes a gradual diminution through the day. In both sexes, the effect produced by *change* of posture increases with the usual frequency of the pulse, whilst the exceptions to the general rule are more numerous, as the pulse is less frequent. The variation is temporarily increased by the muscular effort, involved in the absolute change of the posture; and it is only by the use of a revolving board, by which the position of the body can be altered, without any exertion on the part of the subject of the observation, that correct results can be obtained. That the difference between standing and sitting should be greater than that between sitting and lying, is what we should expect, when we compare the amount of muscular effort required in the maintenance of the two former positions respectively. A different explanation has, however, been offered by Ludwig, who considers that the slowing of the pulse which occurs in the recumbent position is due to excitation of the vagal roots from increased blood-pressure in the medulla, and Dr. Brunton has observed that if whilst in the recumbent position the head be held much lower than the body the pulse becomes greatly accelerated, possibly from excitation of the accelerator centres in the medulla. It is stated by Lichtenfels and Frölich that the alternate contraction and relaxation of any set of muscles has a much greater effect than their simple tonic contraction in increasing the action of the heart.†

prevalent notion, has been determined by the observations of Levret and Mitivié ("De la Fréquence des Pouls chez les Aliénés"), Dr. Pennock ("Amer. Journ. of Med. Sci.," July, 1847), and Prof. Volkmann (Op. cit., p. 427).

* "Guy's Hospital Reports," vol. iii. p. 312; and "Cyclop. of Anat. and Physiol.," vol. iv., Art. 'Pulse.' † "Denk. d. kais. Akad. d. Wissens. zu Wien," 1852, t. iii. pt. ii. p. 149.

e. The pulse is well known to be much accelerated by *Mental Excitement*, especially by that of the Emotions; it is also quicker during *Digestion.* The ingestion of warm food produces this effect much more rapidly than cold; and according to Budge,* whilst animal food raises the frequency of the pulse more quickly than vegetable, the effect of the latter is much greater and more permanent. Lichtenfels and Fröhlich found that, an hour and a half after breakfast, the pulse was 13 beats per minute quicker than before, whilst there was only an increase of 9 beats an hour after dinner. The pulse was less frequent in vegetarians, however, than in those who fed on animal diet, and was probably less energetic. The ingestion of large quantities of water diminishes the frequency of the pulse (Bocker). Dr. Ed. Smith ascertained the rate at each hour of the 24 hours for 3 days successively in health, and for 6 days in Phthisis. He found that it was never stationary, but that there was a progressive increase after a meal and decrease before a meal, so that there were four maxima and four minima daily. The maxima occurred about two hours after a meal, and were the greatest after breakfast and after tea. The day minima immediately preceded the meals, and all were nearly equal. The pulse invariably fell after 9 P.M., so that supper produced but little effect; and the lowest point of the 24 hours was from 3 to 5 A.M. There was an increase in the morning with sunlight. The difference between the maximum of the day and the minimum of the night amounted in health to from 14 to 34 pulsations, and in Phthisis to from 22 to 45 pulsations. The increase from that of the night to the breakfast maximum was, on the average, 27 pulsations in phthisis. There was a considerable increase in children whilst eating. During a fast of 24 hours the variation in the rate was small, but there was an increase during the usual meal hours and an increase at night.

f. The pulse varies also with the *Season*, and Dr. Ed. Smith has shown by daily experiments throughout the year that the rate of pulsation is greater in the Spring and Summer than in the Winter, both in health and Phthisis. In experiments made upon Frogs, Budge† and Calliburcés found that immersion of the excised Heart or of the hind legs in warm water increased the frequency of the pulse (§ 243); the same result was obtained after section of the Crural Nerves, or after poisoning by Curare, showing that it was not effected through the cerebro-spinal nervous system.

g. Variations in the pressure of the surrounding atmosphere exert a certain, but not very well-ascertained influence on the frequency of the Pulse. Alpine travellers are well acquainted with the increased rapidity of the pulse which occurs on attaining great heights; but this is probably in great measure attributable to the great muscular exertion previously made. Salvatore Tommasi, however, observed an increase of 8 in the number of his pulsations, after a good night's rest in the Alpi di Susa, at an elevation of between seven and eight thousand feet.‡ In some experiments performed by Vivenot§ on the effects of compressed air, in which the barometer rose from 742 mm. to 1060 mm., the pulse was observed to rise 3.45 beats on an average of 79. After exposure for an hour and a half to the maximum of pressure it rose 6·33 beats, and 7·31 beats on return to the ordinary pressure. In other experiments on the influence of rarefied air, the barometer falling from 758 to 500 mm., there were observed an increase in the amplitude of the radial tracings, as shown by the sphygmograph, indicative of diminution of vascular tension; increased feeling of warmth in the skin, especially of the face; con-

* "Physiologie," 1861, p. 275. † Ibid., p. 272. ‡ "Fisiologia," 1861, p. 244.
§ Virchow's "Archiv," xxxiv. p. 515. See also the Essays of Bucquoy and Pravaz, on this subject.

gestion of the conjunctiva; uneasiness in the head, difficulty of thinking, and neuralgic pains in the forehead, neck, and teeth; all which symptoms appeared to arise from derivation of the blood to the cutaneous capillaries. On gradual readmission of the air they soon vanished.*

232. It may be advisable briefly to sum up the circumstances affecting the frequency of the heart's action. As has already been pointed out the heart not only possesses an internal system of ganglia and nerves by which its movements can be maintained and regulated for some time after excision from the body, but it is also under the control of centres situated in the medulla oblongata; and as there is reason for believing that there are both accelerating and inhibitory centres in the heart and in the medulla, it is obvious that great difficulty must exist in determining the cause of any particular variation in the frequency of its beats that may be observed. We have, however, evidence that the heart may be influenced—

A. By conditions affecting the *intra-cardiac motor ganglia*, which may be (1) excited, and the frequency of the pulsations increased—*a*, by heat; *b*, by mechanical, chemical, and electrical excitation; *c*, by increased blood-pressure, which is essentially a mechanical irritant; *d*, by various poisons: or (2) depressed, and the pulsations lowered—*a*, by cold; *b*, by diminished blood-pressure; *c*, by certain poisons, as chloral.

B. By conditions affecting the *intra-cardiac inhibitory ganglia*, these being stimulated and the heart slowed or stopped in diastole by certain poisons (Muscarin) and paralysed by others (Atropin).

C. By conditions affecting the *intra-cardiac accelerator ganglia*, leading to increased frequency of action. At present these cannot be satisfactorily distinguished from those affecting the intra-cardiac motor ganglia.

D. By conditions affecting the cardiac *inhibitory centres in the Medulla oblongata*, such as increased blood-pressure, which acts directly upon them,† or by irritation of the depressor nerve, or of various other sensory nerves, which act upon them in a reflex manner, or by the action of poisons (Digitalis), all of which excite these centres and cause slowing of the heart's action.

E. By certain conditions affecting the accelerator centres in the medulla, as diminished blood-pressure, mental processes, the action of poisons. They may also probably be excited in a reflex manner. It will be seen from the above that certain conditions, increased blood-pressure for example, exerts a double action on the cardiac nerves. On the one hand, it excites the heart to increased

* A. Jaminet, "On the Physical Effects of Compressed Air on Man," &c. (Pamphlet), 1871, pp. 135. Jaminet had the opportunity of examining the effects of compressed air on many workmen engaged in the construction of the Illinois and St. Louis Bridge over the Mississippi River. In this work the men were exposed to a pressure at one time of 50lbs. to the square inch, exclusive of the 15lbs. of the ordinary ambient atmosphere. It was found necessary at an early period to construct an air-lock or intermediate room, where the passage into air or ordinary pressure could be gradually effected, otherwise most serious symptoms, great muscular exhaustion, headache, epigastric pain, sickness, paralysis, hæmorrhage, and even death resulted. M. Jaminet found that increased frequency of the pulse and respiration occurred during the first few minutes, the pulse rising about 15 beats above the normal; but after remaining in the air-chambers for two hours, and whilst still exposed to the action of the increased pressure, the pulse fell about 15 beats below the normal. On issuing into the open air the pulse again rose to 15 or 20 beats above the normal, and slowly in the course of an hour or two returned to its usual state. Glaisher, in his scientific balloon ascents (see his article on Aeronautics in the "Encyclopædia Britannica," 9th edit. 1875, p. 197), found that the pulse, which was 76 before starting, increased considerably at high altitudes, being 90 at 10,000 feet, 100 at 20,000 feet, and 110 at greater heights.

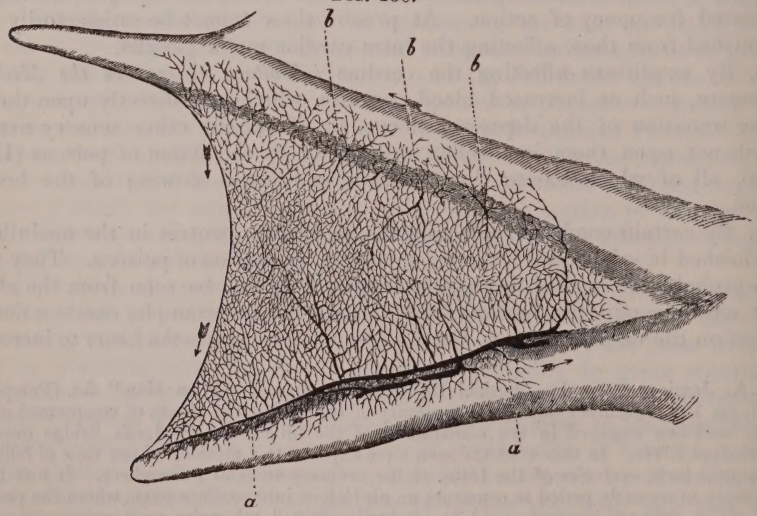
† See Drosdow, "Petersburg Med. Anzeiger," No. 36, 1875; also Tschirjew, Du Bois Reymond's "Archiv f. Physiol." 1877, p. 116.

frequency of action by direct irritation of its motor ganglia through filaments distributed to the Endocardium; on the other hand, it stimulates the vagal centres in the Medulla, and thus causes slowing of the heart, the actual result in any given case being dependent upon the preponderating influence of the cardiac motor or medullary inhibitory centres. Usually the medullary centres are strongest, and increased blood-pressure causes slowing of the heart; but if the vagi be divided, so that they can no longer act on the heart, increased blood-pressure stimulates the heart to more rapid action. The increased rapidity of the pulse observed by Asp to follow excitation of the central extremity of the divided spinal cord has not been found to be constant by Dittmar,* the variation being probably dependent upon the complicated effects of the increased blood-pressure, which the latter experimenter has shown results from this operation.

3. *Movement of the Blood in the Arteries.*

233. The Blood propelled from the Heart is distributed to the body in general by a system of Arteries, which may be likened in its arrangement to the trunk and branches of a tree, except that very frequent communications or anastomoses exist among these branches, so that, by continual subdivision and inosculation, their distribution comes more and more to resemble the capillary network in which they terminate (Fig. 130). Although the *diameters* of the branches, at each subdivision, together exceed that of the trunk, yet there is but little difference in their respective *areas*. What difference does

FIG. 130.



Web of *Frog's foot*, stretching between two toes, magnified 3 diameters: showing the blood-vessels, and their anastomoses:—*a*, *a*, veins; *b*, *b*, *b*, arteries.

exist, however, is, with few exceptions, in favour of the branches; and thus it happens that there is a gradual increase in the capacity of the arterial system from its centre towards the capillaries, whose capacity is many times greater. In passing from the Capillaries to the smaller arteries, the thin wall of the former, composed of a single layer of cells, becomes strengthened by a second layer of flattened nucleated cells placed externally, and forming a *tunica*

* Ludwig's "Arbeiten," 1871, p. 18.

adventitia; short unstriped muscle-cells also appear, which are at first irregularly distributed, but subsequently form a continuous circular layer—the *Tunica media.* Between the muscle layer and the original endothelial wall of the capillary a delicate hyaline elastic membrane, the *Tunica intima*, can be recognised. In *larger vessels* the tunica adventitia or outer coat is vascular, and composed of connective with much elastic tissue. Surrounding the fasciculi of the connective tissue are lymph spaces, containing branched connective tissue-cells. The tunica media is composed of many layers of short muscular fibre-cells, which in the largest trunks are separated by hyaline elastic membranes and plexuses. Between the outer and middle coat in the larger vessels is a special elastic membrane, the external elastic coat of Henle. The tunica intima is composed of a series of fenestrated laminæ. Between the tunica intima and the endothelium is a membrane composed of connective tissue, named the "subendothelial connective tissue" membrane. Longitudinal muscular fasciculi have been observed in the adventitia of the splenic, renal, femoral, mesenteric, and popliteal arteries; and in the tunica media of the hepatic, splenic, crural, mesenteric and umbilical. Bardeleben, indeed, maintains that all large and middle-sized arteries possess an inner longitudinal muscle-coat.* The adventitia is relatively thickest in the minute arteries. The media is in all arteries the most conspicuous coat. The intima increases in thickness towards the aorta. The endothelium everywhere consists of a single layer of cell plates.†

234. The arteries exert a most important influence upon the movement of the blood through them in virtue of the physical and vital properties of their walls. Their *elasticity*, which is a physical property that persists after death until a serious change takes place in their composition, is due to the elastic fibres their walls contain, whilst their property of *contracting* on the application of a stimulus so long as their vitality remains is attributable† to their muscular coat. These two endowments are possessed in various degrees, proportional to the respective predominance of the elastic or of the muscular tissue, by the different parts of the Arterial system. Thus, as was justly remarked by Hunter, the *elasticity*, being the property by which the interrupted force of the Heart is made equable and continuous, is best seen in the large vessels more immediately connected with that organ; whilst, on the other hand, the *contractility* is chiefly observable in the smaller vessels, where it is more required for regulating the flow of blood towards particular organs. With the exception of the capillaries, *nerves* partly consisting of medullated and partly of pale or non-medullated fibres have been demonstrated in all vessels, even in the non-muscular veins of the pia mater. The fibres,‡ after they have traversed the tunica adventitia, break up into a fine network with here and there ganglionic cells and knots. It is to these ganglionic enlargements that the local contractions of the vessels are due, which take place when the main trunks from the sympathetics supplying them have been divided.

235. The chief purpose served by the *Elasticity* of the Arteries is one of

* See Prof. Kölliker's "Manual of Human Histology" (Sydenham Society's edit.), vol. ii. p. 291, and "Handbuch der Gewebelehre," 5 Auflag. p. 583. Eberth in Stricker's "Human and Comp. Hist.," Syd. Soc. Trans., 1870, vol. i., Art. 'Blood-vessels.' Klein and Noble, "Atlas of Histology."

† Wundt ("Physiologie," 1873, p. 287) finds the co-efficient of elasticity of the arteries (*i.e.*, the weight necessary to be applied to double the length of a given piece) to be 1120 grains, and that of the veins 1465 grains. In both sets of vessels the elasticity is greater in the longitudinal than in the transverse direction. The co-efficient of elasticity of the aorta, taking the mean of several experiments, is 927 grains in the direction of its length and 588 grains in the direction of its breadth, whilst that of the jugular vein is 1503 grains in the former and 725 grains in the latter direction.

‡ Eberth, in Stricker's "Hum. and Compar. Histol.," Syd. Soc. Trans., vol. i. p. 266.

a purely physical character; its effect being to convert the intermittent impulses, which the blood receives from the heart, into a continuous current. The former are very evident in the larger trunks; but they diminish with the subdivision of these, until they entirely disappear in the capillaries, in which the stream is usually equable or nearly so. If a powerful force-pump be made to inject water, by successive strokes, into a system of tubes with unyielding walls, the flow of fluid at the farther extremities of these tubes is as much interrupted as its entrance into them. But if water be forced by a syringe into a long tube of caoutchouc, for example, the stream is found to be equalized before it has proceeded far, owing to that part of the force which is not expended in propelling the fluid, but is employed in stretching the elastic walls, being again restored when the distending force ceases to act. This effect is in fact accomplished, at any part of the Arterial circulation, in a degree proportionate to its distance from the Heart; and in this mode it is, that the intermittent force of the ventricular contraction is almost equably distributed over the whole of the interval between one systole and another, by the contraction of the elastic tubes in the dilatation of which it was at first expended. Another effect of this elasticity is to enable the vessels to accommodate themselves to the various movements of the body and limbs, without interference or obstruction to the current of blood traversing them.

236. The *contractility* of the arteries fulfils several important purposes. It is the principal means by which hæmorrhage from the smaller vessels is arrested after injury, and even in the case of so large an artery as the temporal, the complete division of the tube is often the readiest means of checking the flow of blood. Secondly, under the influence of the nervous system it regulates the supply of blood to the different tissues and organs of the body in accordance with the variations of their functional activity. And, lastly, it enables the whole vascular system to accommodate itself to the very varying amount of fluid it contains at different times, so that the pressure under which it is distributed through the body is approximately the same. It may be readily demonstrated by experiment. Thus, when a ligature is placed upon an artery in a living animal, the part of the artery beyond the ligature becomes gradually smaller, and is emptied to a certain degree, if not completely, of the blood it contained. Again, when part of an artery in a living animal is isolated by means of two ligatures, and is punctured, the blood issues from the orifice, and the inclosed portion of the artery is almost completely emptied of its contents. This contraction is much greater than could be accounted for by the simple *elasticity* of the tissue; and is more decided in small than in large vessels. The empty condition of the arteries, generally found within a short time after death, seems to be in part due to the same cause; since their calibre is usually much diminished, and is sometimes completely obliterated. A remarkable example of the same slow contraction is that which takes place in the end of the upper portion of an arterial trunk, when the passage of blood through it is interrupted by a ligature; for the current of blood then passes off by the nearest lateral branch, and the tube of the artery shrivels and soon becomes impervious from the point at which the ligature is applied back to the origin of that branch. This last fact is important, as proving how little influence the pressure of the blood possesses over the calibre of arterial tubes, since without any interruption to the pressure of blood occasioned by it the tube becomes impervious. Other evidence of the contractility of the arteries may be readily obtained by observing the effects of various stimuli, mechanical, chemical, or electrical, upon the vessels of a transparent membrane, such as the bat's wing or the frog's foot. Thus if,

whilst watching the movement of blood in a companion artery and vein, we draw the point of a fine needle across them three or four times, without apparently injuring them or the membrane over them, they will both presently contract and close; then, after remaining for a few minutes in the contracted state, they will begin again to dilate, and will gradually increase in diameter until they acquire a larger size than before the stimulus was applied. When in this condition they will not again contract on the same stimulus as before; the needle may now be drawn across them much oftener and more forcibly, but no contraction ensues, or only a trivial one, which is quickly followed by dilatation; with a stronger stimulus, however, such as that of great heat, they will again contract and close, and such contraction may last more than a day, before the vessels again open and permit the flow of blood through them.* Further, it has been ascertained by the experiments of Poiseuille (which confirm those of John Hunter), that when an artery is dilated by fluid injected into it, it reacts with a force superior to the distending impulse; and that, if a portion of an artery from an animal recently dead (in which the contractility is preserved), and one from an animal that has been dead some days (in which nothing but the elasticity remains), be distended with an equal force, the former becomes much more contracted than the latter, after the distending force is removed.

237. There is no sufficient proof that the contractility of the arteries enables them to exert a *propulsive* action in any marked degree supplementary to that of the Heart; and yet, looking to the general facts already stated, as to the diffusion of the propulsive power through the arterial trunks in many of the lower animals, their experimentally-proved reaction upon a distending force, and to the circumstance, that a kind of rhythmical action, occurring seven or eight times in the minute, has been observed by Wharton Jones in the vessels of the Bat, by others† in those of the ear and saphenous artery of the Rabbit, which last contracts one or twice in the minute, and in the vessels of the web of the foot in the Frog, it does not seem by any means improbable that some such power should be preserved, even where there is the greatest concentration of the propulsive force in the muscular walls of the Heart. It is important to notice that these systolic and diastolic movements of the vessels are not simultaneous on opposite sides of the body, and that they are quite independent of cerebro-spinal innervation, since they continue even when the whole of the cerebro-spinal and sympathetic nerves have been divided, and even after division of the spinal cord itself in the neck.‡

238. The *influence of the Nervous system* upon the calibre of the vessels, which might be inferred to exist from the act of blushing and other analogous phenomena, is capable of experimental demonstration. Thus the application of a stimulus, such as an induced current of electricity§ to the sympathetic trunk on either side of the neck, causes contraction of the minute arteries on that side of the face, which can be well seen in those distributed to the external

* See Sir James Paget's "Lectures on Surgical Pathology," vol. i. pp. 302, 303.—As Sir James Paget justly remarks, it is from the mechanical stimulus of the knife that small divided vessels contract and close, so as speedily to cease bleeding; but this contraction lasts only for a time; and hæmorrhage would commence on their dilatation if their mouths were not sealed by coagula of blood or lymph. When secondary hæmorrhage does occur from want of such coagulation, it is most effectually controlled by the application of such stimuli as the actual cautery, which induces a more prolonged contraction of the vessels.

† Lovén, Ludwig's "Arbeiten," 1866, p. 1; Riegel, Pflüger's "Archiv," 1871; Saviotti, Virchow's "Archiv," Band l., 1870; Gunning, "Onderzoeckingen," &c., Utrecht, 1857.

‡ See Brunton, in Ludwig's "Arbeiten," Band iv., 1870, p. 106.

§ See Waller, by whom this experiment was first made, in "Comptes Rendus," 1853, t. xxxvi. p. 378.

ear of the cat or rabbit; whilst, on the other hand, section of this nerve leads to their dilatation. As in the case of the Heart, the nerves supplying the blood-vessels appear to have two centres, one of which is represented by the small ganglia distributed in the walls of the vessels, whilst the other is represented by a centre, or a series of centres, situated in the medulla oblongata and spinal cord. The activity of the *local* ganglia is rendered evident by the contractions that may be produced by direct irritation after division of all the nerves supplying a part. The *central* ganglia governing the contraction of the vessels have received much attention during the last few years,* the general result of which has been to show that an important centre is situated in the medulla oblongata, its lower limit in rabbits being about one-eighth of an inch above the level of the apex of the calamus scriptorius, whilst the upper limit is near the upper border of the corpus trapezoides, just below the corpora quadrigemina. It occupies the antero-lateral part of the medulla oblongata on each side, and corresponds to the continuation through the medulla oblongata of the anterior part of the spinal cord.† In some animals, and especially in the Frog, the vaso-motor centre or centres must extend for some distance down the spinal cord, since on division of the cord in the cervical region which is followed by dilatation of the vessels generally, and by diminution of the blood-pressure in them, section of such a nerve as the sciatic is followed by still further dilatation of the vessels of the posterior limbs accompanied by elevation of temperature. Some experiments of Cyon seem also to show that the vaso-motor centre extends into the brain above the plane of the medulla oblongata. Stricker fixes its limits, in the dog, between the fifth cervical nerve and the first dorsal nerve. This centre exercises a permanent tonic influence on all the smaller vessels, and especially upon the smaller arteries of the body, maintaining their muscular fibres in a state of gentle contraction. It receives centripetal or afferent, and gives off efferent or centrifugal fibres. Both sets of fibres, as Miescher‡ and Nawrocki§ have shown, run in the lateral columns of the spinal cord, and enter into or issue from it with the roots of the several spinal nerves, at least as low down as the eleventh dorsal nerve. They run partly in the sympathetic cords, and partly with the branches of the spinal nerves. Thus the cervical cord of the sympathetic contains the vaso-motor nerves of the skin of the head, the conjunctiva, and salivary glands. The splanchnics, which are exceedingly important vaso-motor nerves, supply the very dilatable vessels of the abdominal viscera. After they have been divided, the abdominal vessels become greatly distended with blood, and retain so much of it in their interior as to lower the pressure in the carotid to a very considerable extent. This effect is

* "Wiener Sitz.-ber.," Band xlix., and "Zeit. f. Rat. Med.," Band i. For other papers on the influence of the nerves on the blood-vessels, see besides many of those mentioned in the note on p. 320, the essays of Ludwig in conjunction with Cyon, Lovén, Asp, Hafiz, Owsjannikow (1871), and Dittmar (1873), in Ludwig's "Arbeiten," 1866–73, and "Berichte der Sächs. Gesell.," 1866–71. Also the papers of v. Bezold in conjunction with Stezinsky, Bever, Breymann, Dreschfeld, and Gescheidlen, in the "Untersuch. aus der Physiol. Labor. zu Würzburg;" Heidenhain, in Pflüger's "Archiv," Band iii. iv. and v.; Röver, "Nerven einfluss auf. d. Gefässe," 1869; Thiry and Kowalewsky, "Centralblatt," 1868, p. 579; Saviotti, Virchow's "Archiv," Band l. 1870, p. 592; Budge, Pflüger's "Archiv," 1872, p. 303; Goltz, Pflüger's "Archiv," Band viii. p. 460; Putzeys and Tarchanoff, "Centralblatt," 1874, p. 641; Putnam, "Boston Med. and Surg. Journal," 1870, p. 469; Bernstein, Pflüger's "Archiv," Band xv. p. 575; Grützner, idem., Band xvi. 1878, p. 1; Stricker, "Wien. Acad. Sitzungsber.," Band lxxv. 1877.

† "Journal de la Physiologie," t. i. 1858, p. 209. See also Vulpian, "Leçons sur l'Appareil Vaso-moteur," 1875, p. 266; and Cyon, 'Hemmungen und Erreg, in Central Syst. d. Gefässnerven,' "Bull. d. Petersb. Akad.," Band xvi. p. 97, and "Centralblatt," 1871, p. 407.

‡ Ludwig's "Arbeiten," 1870, p. 172. § Idem., 1871, p. 89.

not, however, permanent, the pressure rising again as the vessels recover their tone, and by the contraction of their coats drive their contents into the general system again. The contraction is probably attributable to the action of the minute ganglia found in the vascular walls. If, after division of the splanchnics, an electric stimulus be applied to their peripheric extremity, the vessels of the abdominal viscera contract and the blood-pressure in the carotid rapidly rises. The vaso-motor nerve-fibres for the upper extremities pass from the roots of the middle dorsal nerves to the sympathetic cord, and thus reach the first dorsal ganglion, from whence they pass into the brachial plexus (E. Cyon). Those for the lower extremities proceed from the rami communicantes of the sympathetic into the anterior roots of the spinal nerves.* The vaso-motor centre is capable of being excited and of being depressed. In the former case the smaller arteries either of a definite region or of the whole body contract, and the blood-pressure rises. In the latter case the smaller arteries of a territory of variable extent dilate or relax and the blood-pressure falls. This effect is in most instances due to the accumulation of blood in the veins of the abdominal viscera. The excitation of the centre indicated by exaltation of the blood-pressure in the arteries can be effected by the circulation through its vessels of blood charged with carbonic acid or deficient in oxygen, and in a reflex manner by the irritation of almost any of the sensory nerves, as those of the skin,† peritoneal layer of the stomach,‡ dura mater,§ olfactory or nasal nerves‖ (providing the brain is uninjured, Cyon); also by irritation of the cervical sympathetic nerve,¶ and by certain poisons, amongst which digitalis may be particularly mentioned.** On the other hand, the vaso-motor centre can be depressed, or its action inhibited, by irritation of the depressor nerve of the vagus, and fibres having a similar depressing action run in the vagus below the origin of the nervus depressor from the vagus. The *depressor nerve*†† in the Rabbit springs, as already mentioned, by two roots from the superior laryngeal nerve and from the trunk of the vagus, and either runs to the inferior cervical ganglion, or after a short course is blended with the vagus or sympathetic trunk, or passes to the cardiac plexus. If it be divided, stimulation of its central end causes diminution of pressure in the whole arterial system and slowing of the pulse, phenomena that are to some extent independent of each other; for if the pneumogastric be first divided in this experiment no change occurs in the frequency of the pulse,

* The nerves of the vessels supplying a muscle do not always accompany the motor-trunks of that muscle. Thus, the biceps femoris receives its motor nerves from the sacral plexus, but its vaso-motor nerves come from the lumbar plexus through the crural nerve.

† Lovén. ‡ Mayer and Pribram, "Sitz.-ber. d. Wien Akad.," Band lxvi. 1872.

§ Ludwig and Dittmar, Ludwig's "Arbeiten," 1870, p. 4.

‖ Hering and Kratschmer; Rutherford, "Journal of Anat. and Phys.," 1873, vol. vii. p. 283; Brown-Séquard, "Archives of Scientific Med.," 1873, p. 90.

¶ Aubert and Roeven, "Kritische Untersuch.," &c. Rostock, 1869.

** Brunton and Mayer, "Journ. of Anat. and Phys.," Nov. 1872. Callenfels ("Zeits. f. Rat. Med.," 1855, Band vii. p. 191) has noticed contractions of vessels of one ear of a rabbit occur when the opposite ear was pinched; and Brown-Séquard ("Journ. de la Physiol.," 1858, p. 504) observed that on immersion of one hand in cold water the temperature of the other uniformly fell, in one instance as much as 21° F.: a result which may perhaps serve to explain the effects of the application of cold in controlling hæmorrhage when applied to some distant part of the body.

†† Discovered by E. Cyon. See "Ber. d. k. Sächs. Gesellschaft. d. Wiss.," October, 1866. See also Bernhardt, "Anat. u. Physiol. Untersuch. üb. den Nerv-dep. bei der Katze Diss.," Dorpat, 1868. Kowalewsky and Adamük, "Centralblatt f. d. Med. Wiss.," 1868, p. 545; Roever, "Krit. u. exper. Unters. der Nerveneinflüssen auf die Blutgefässe," Rostock, 1869; also "Centralblatt," 1868, p. 577. Kreidmann, idem, 1878, p. 193, finds anatomical reasons for believing that it forms part of the vagus trunk in man. Baxt, "Ueber die Stellung des N. Vagus zum N. Accelerans cordis. Leipziger Berichte," 1875, p. 323.

whilst the pressure invariably falls. Stimulation of the proximal extremity of the cut depressor nerve is not followed by any perceptible effect.* The nerve seems to act essentially on the vaso-motor centres and not on the heart; since its depressing influence is still observed after division of all the nervous connections between the heart and the brain and medulla, whilst it is scarcely noticeable after division of the splanchnics, since the abdominal vessels are then fully distended. It occurs in curarized as well as in non-curarized animals. It is possible that instead of acting as an inhibitor of the vaso-motor ganglia, it may stimulate the vaso-dilator ganglia, if such ganglia exist; but in either case its action is chiefly exerted on the abdominal vessels and upon those of the inferior extremities, since if the aorta be compressed first below the diaphragm no marked effects are produced. The influence of the depressor nerve in securing a uniformity of pressure throughout the vascular system is sufficiently clear, for if in consequence of stimulation of the vaso-motor centres the peripheric arteries have contracted and the blood-pressure has risen beyond a certain point, this blood-pressure affecting the heart distends its walls and excites the *depressor nerve*. The depressor reacting on the vaso-motor centre in the medulla inhibits its action, which leads to dilatation of the blood-vessels and a fall in the blood-pressure. The term "Traube's curves" is applied to the rhythmical variations of arterial pressure which were observed by Traube† to occur in animals under the influence of Curara during the gradual rise of pressure that arises after complete cessation of the respiratory movements and section of both vagi. Kowalewsky and Adamük and Hering have shown that the rise and fall of pressure constituting Traube's curves are independent alike of variations in the heart's action, and of asphyxia, and that they are referrible to the circulation of non-arterialized blood through the vaso-motor centres, and to variations in the tone of the vessels.

239. There are certain nerves the irritation of which causes dilatation of the vessels to which they are distributed. This is the case with the chorda tympani and with the nervi erigentes of the penis (Lovén), and there is considerable difficulty in explaining their action. The most reasonable view is that of Vulpian, who supposes that there are inhibitory centres in the walls of the vessels which, when irritated, restrain or abolish the tonic influence of the vaso-motor centre, and dilatation is the immediate consequence.‡ Other views that have been advanced are:—1. That of Schiff, who believes it to be possible that certain nerves may, instead of causing contraction, cause elongation of muscular fibres. 2. That which attributes the dilatation of the arteries to increased blood-pressure caused by contraction of the veins; but this is contrary to fact, the veins being dilated in all cases. 3. That of M. Legros,§ who regards active congestion as the result of increased peristaltic contraction of the vessels. 4. That it is due to increased attraction of the tissues for the blood, so that a suction-force or *vis a fronte* is established. Some remarkable experiments bearing on the subject of dilatator-fibres were made in 1876 by Max Frey;‖ who arrived at the conclusion that such fibres were present in the chorda tympani nerve. His method consisted in determining the flow of blood from the divided vessels before, during, and after stimulation of the sympathetic

* Beaunis, "Nouveaux Elements de Physiologie," 1876, p. 966.

† "Allgemein. Med. Centralzeitung," Nos. 9, 30, 89, 99, and "Centralblatt," 1865, p. 881. See also Thiry, "Sitz.-ber. d. Wien. Akad.," 1864, p. 32; Kowalewsky and Adamük. "Centralblatt," 1868, p. 545; Hering, "Sitz.-ber. d. k. Akad. zu Wien.," Band lx. 1869; Sanderson, in "Handbook to Phys. Lab.," p. 317, 1873.

‡ Vulpian, "Leçons sur l'Appareil Vaso-moteur," 1875, p. 177 *et seq.*; Frey, "Sächs. Akad. Sitzungsber.," Band xi. p. 89. § Legros, "Thèse," 1873.

‖ Ludwig's "Arbeiten," 1876, p. 91; see also Solyet, "Gaz. Med.," 1878, No. 46.

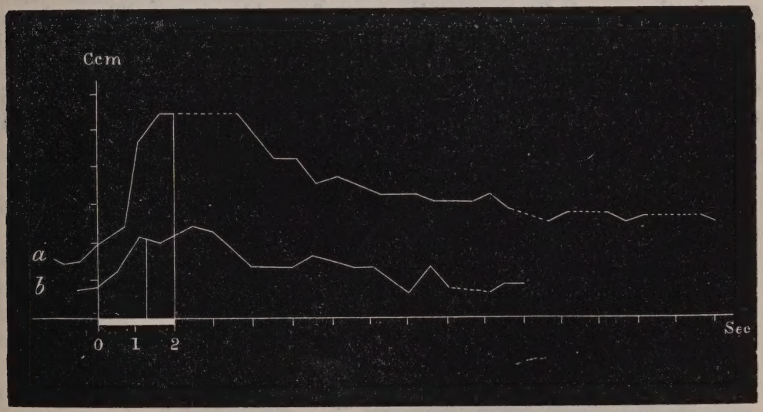
and chorda tympani nerves, and several of his tracings are here given. It is possible that the nerves effecting dilatation of the vessels may exert their

Fig. 131.

The Abscissa is here divided into sections representing ten seconds. The broad white line indicates the period during which a powerful electrical stimulus was applied to the sympathetic nerve. Each millimetre of the ordinals in height corresponds to the discharge of 0·2 cubic centimetre of blood. It will be seen that immediately after the application of the stimulus there was a rise which represents the sudden contraction of the arteries forcing onward their contents; the line then rapidly descends and reaches a minimum which lasts long after the stimulus has ceased to be applied, and rises again by fits and starts. This drawing demonstrates that the stimulation of the sympathetic causes great contraction of the smaller arteries.

influence upon the longitudinal muscular fibres already stated (§ 233) to exist in many arteries. The mode in which variations of pressure affect the pulse has already been explained, § 232.

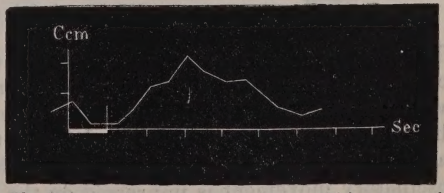
Fig. 132



This Figure shows the effect of powerful stimulation of the Chorda tympani nerve in modifying the discharge of blood from a vessel. The curves *a* and *b* show the results of two successive stimulations of the chorda. The stimulus was applied during the time marked 0 to 2 on the abscissa in the first stimulation, the effect of which is represented by *a*, and from 1 to 2 in the second stimulation, the effect of which is represented by *b*. There is a latent stage varying from 2·5 to 0·1 second in both.

240. The distension of the Arteries that is consequent upon the intermittent injection of blood into their trunks gives rise to the *pulsation* which is perceptible to the touch in all but the smallest arteries, and which is visible to the eye when they are exposed. It would seem to the touch, as if this were chiefly effected by an increase of *diameter*, and the experiments of Volkmann ("Hämodynamik") led him to believe that the transverse dilatation is greater

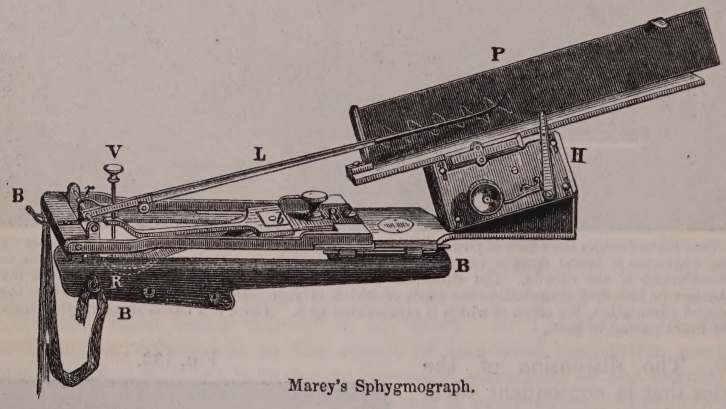
Fig. 133.



The dark line shows the period during which a powerful electrical stimulus was simultaneously applied to the sympathetic and to the chorda tympani nerve. It is seen that the sympathetic first responds to the stimulus as in Fig. 131, overcoming the chorda, but the chorda subsequently exerts its full action.

than the longitudinal; but these experiments were made under conditions so different from those of the living artery, that but little weight can be attached to them. It is to be remembered, however, that every increase in length augments the capacity in only a *simple* ratio; thus a tube of 21 inches in length will only contain *one-twentieth* more than a tube of 20 inches long, of the same diameter. On the other hand, every increase in diameter augments the capacity of the tube in the ratio of the *square* of that increase; thus the capacity of a tube of 21 lines in diameter will be to that of a tube of 20 lines, as 441 : 400, or *one-tenth* more. Consequently, supposing the increase of *capacity* to take place equally in both directions, the increase in longitudinal *dimension* will be far more apparent than the *transverse* enlargement. The total increase of capacity was estimated by Flourens, from experiments upon the carotid artery, at about 1-23rd part; but it is affirmed by Volkmann* that this must not be considered by any means a constant ratio, since it varies in different arteries, and in the same artery under different circumstances. It has also been attributed to *elongation* of the artery, which was supposed to be lifted from its bed at each pulsation, and, when previously straight, to become curved; the impression made upon the finger by such displacement, not being distinguishable from that which would result from the dilatation of the tube in diameter. A very obvious example of this upheaval is seen in the prominent temporal artery of an old person. The real cause of the sensation given by the pulse to the observer, however, may be considered to be the return of the artery to a cylindrical form under increased internal pressure, after it has been more or less flattened by the pressure of the finger against an unyielding structure, while in a comparatively flaccid condition.

Fig. 134.



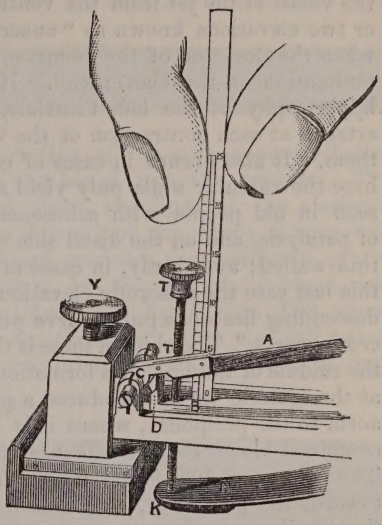
Marey's Sphygmograph.

The production of the pulse is a subject of much interest. The passage of a continuous current of fluid through an elastic tube takes place in accordance with the same laws as those which govern its passage through a rigid tube; but if into an already tightly-filled elastic tube which is closed at its extremity a jet of fluid be driven, the first part of the tube undergoes distension, and an oscillatory movement is impressed on the particles of the fluid, which rapidly propagates itself in the form of a positive wave to the extremity of the tube, and is then reflected to and fro along the tube till it dies out. In this case there is only an oscillation of the particles of the fluid, but no translation of

* Op. cit., chap. xiv.

them. If, however, the extremity of the tube be open, and a jet or succession of jets of fluid be forced into it whilst the fluid it contains is in motion, the result is a combination of undulatory movement with current movement. The velocity of the wave is proportional to the elasticity of the tube; it varies inversely with the density of the liquid; it diminishes gradually with the length of the tube, and it increases with the rapidity of impulsion of the fluid.* The amplitude of the wave is proportional to the quantity of fluid which penetrates into the tube and the briskness of the jet. It diminishes as the wave advances.† The fluctuations of the Pulse in the living body without exposure of the artery can be rendered apparent by the use of an instrument originally invented by Vierordt, but materially modified and improved by Marey, termed the Sphygmograph. The general arrangement of the instrument is shown in Fig. 134, where the part B B is applied to the forearm, whilst the pressure on the artery is effected by a very light steel spring, terminating in a small plate of ivory R, capable of elevation or depression by the screw V. The long arm of the wooden lever L terminates in a fine point touching the plate of smoked glass, or glazed card P, which is made to move gradually forwards by clockwork in the box H. The immediate descent of the lever after its elevation is accomplished by the very delicate spring at *r*. A modification of Marey's instrument is shown in Fig. 135, by which the pressure exerted on the artery can be approximatively measured. The tracings made by either of these instruments show that under ordinary circumstances the period of ascent or of increase in the tension of the arterial walls is rapid; whilst the period of decrease, during which the elasticity of the larger arteries is acting, is comparatively slow and prolonged.

Fig. 135.



This figure shows a modification of Marey's Sphygmograph, by means of which the amount of pressure exerted on the artery can be approximatively measured. A, registering lever; D, knife-edge on which it rests; K, spring placed over the artery; T, screw regulating the pressure, the amount of which is ascertained by the index B.

Fig. 136.

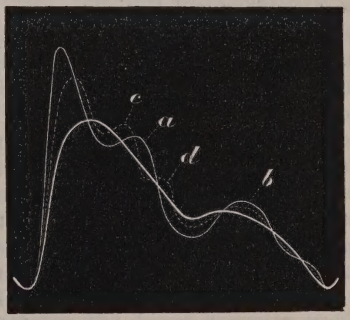


Diagram to illustrate the relation of the Sphygmographic tracing to the true pulse wave. The thick line represents the true pulse wave, the thin line the sphygmographic tracing, the dotted line the tracing drawn by a sphygmograph having a secondary spring to keep down the lever. *a*, first, or dicrotic wave; *b*, secondary wave; *c*, *d*, two small waves into which the tidal wave may be broken by the action of the secondary spring.

* Moens' ("Die Pulscurve, Leiden," 1878) experiments have shown that the rapidity of propagation of a pulse wave in an elastic tube is inversely as the square root of specific gravity of the fluid; that it is also in direct proportion to the thickness of the tube with the same lateral pressure; that it is inversely as the square root of the diameter of the tube with the same pressure; and, lastly, that it is as the square root of the coefficient of elasticity of the wall of the tube with the same pressure.

† See Marey, "La Methode Graphique," 1878, p. 352.

The ascending limb of a pulse-curve is usually steep and uniform; it represents the expansion of the elastic arterial wall consequent upon the entrance into the vessel of the jet from the ventricle. It sometimes, however, presents one or two elevations known as "anacrotic elevations." These occur in general when the duration of the incurrent jet is prolonged beyond the time of an undulation of the elastic wall. It occurs therefore in cases of dilatation and hypertrophy of the left ventricle, when a large jet of blood is driven into arteries at each contraction of the ventricles requiring a long time to distend them. It also occurs in cases of constriction or rigidity of the vessels, since here the vascular walls only yield slowly to the instreaming jet. It is hence seen in old people with atheromatous vessels, after a cold bath, in cases of paralysis, and on the distal side of a ligature when the collateral vessels are thin-walled; and, lastly, in cases of insufficiency of the semilunar valves. In this last case the anacrotic elevation is due to the auricular contraction. The descending limb of a pulse-curve presents two secondary elevations or "katacrotic waves." The chief of these is the "dicrotic" elevation, which occurs about the middle of the line. Its formation is thus explained by Landois:*—As soon as the systolic jet has produced a positive wave rapidly progressing from the aorta to the periphery, where it is lost, the vascular walls contract upon the contained blood, the first effect of which is the closure of the semilunar valves. The column of blood still continuing to be compressed on all sides, streams towards the periphery, but, meeting with resistance, passes back and tightens the semilunar valves to the uttermost, which gives rise to a second positive wave, which again distends the vessels in the direction from the aorta to the smallest arteries, where it is lost. This is the *dicrotic wave*. A third wave may arise in a similar manner, and pursue a similar course, but is only perceptible in the carotids or subclavians, being lost before it reaches the arteries of the lower limbs. It follows from the mode of production of the secondary and tertiary waves that they occur later in proportion to the distance of the artery from the heart. In the carotid, which is the nearest accessible artery to the heart, the dicrotic elevation occurs about 0·35 to 0·37 sec. after the commencement of the pulse. In the Radial, the apex of the dicrotic wave occurs from 0·36 to 0·40 sec. after, and in the dorsal artery of the foot 0·45–0·52–0·59 sec. after the beginning of the pulse, according to the height of the individual. The dicrotic wave becomes smaller and less marked in proportion to the distance of the artery from the heart. It is more distinctly marked in proportion as the systolic contraction is short and vigorous; and, lastly, the height of this wave is great in proportion as the arterial tension is small. Hence it becomes conspicuous during venesection, on exposure to heat, the standing position; whilst it is rendered indistinct by circumstances increasing arterial tension, such as exposure to cold, compression of large trunks, expiration and irritation of vaso-motor nerves.† The fulness of the pulse, or, in other words, the amplitude of the pulsation, is in inverse ratio to the tension of the walls of the vessel; whilst the hardness of the pulse is indicative of arterial tension, and may be produced either by the heart acting with great force and injecting more blood than the arteries can discharge through the capillaries, or by the contraction of the capillaries, themselves preventing the escape of the blood from the arteries into the veins. M. Marey has clearly shown how these two conditions of the arterial system may be induced by acting upon the capillaries alone, and either facilitating the passage of the blood through them, or, on the contrary, rendering it more difficult. Thus the tracing obtained by his

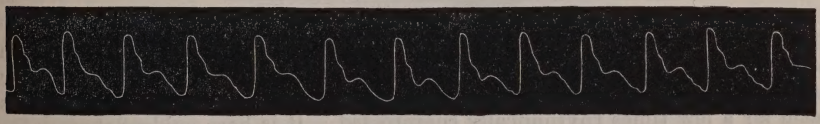
* Landois' "Physiologie," 1879, p. 137. † See Maragliano, "Centralblatt," 1876, p. 27.

Sphygmograph, after exposure to a cold bath of one minute's duration, is shown in Fig. 137. It is that of a hard pulse, in which there is considerable

Fig. 137.

tension of the arterial wall; for the contraction of the cutaneous capillaries constitutes an obstacle to the passage of the blood from the arteries. The line of ascent is accordingly sudden and short, the limit of the elasticity of the vessel being soon reached, and the summit of the curve is rounded; whilst the line of descent is protracted and gradual, the resiliency of the vessel being only capable of reacting slowly on the contained blood, and there is no tendency to dicrotism. On the other hand, Fig. 138 shows the effects of a hot-air bath, and presents the characters of a soft full pulse; a pulse of deficient tension, in which the greater boldness of the curves, their

Fig. 138.



sharper summits, and the marked tendency to dicrotism, may particularly be noticed; as well as the increased frequency of the heart's action, corresponding to the diminished exertion which it has to make in propelling the column of blood through the same vessels. The variations in the curves presented by Sphygmographic tracings have for ages been partially and imperfectly recognised by the *tactus eruditus*, and depend on the vigour and frequency of the heart's action; the fulness of the blood-vessels and degree of elasticity of their walls; and upon the state of relaxation or contraction of the smaller arteries. Thus, amongst others, may be mentioned:—

1. The large compressible pulse of fever, in which the rise and fall of the primary wave curve are sudden. The tidal wave is absent, the dicrotic wave large, and the blood-pressure low. Here the heart's action is vigorous, but the smaller arteries and capillaries are relaxed, allowing the blood injected into them to pass readily into the veins.

2. The large hard pulse of Bright's disease with contracted granular kidney. Here the heart's action is vigorous, but the smaller vessels are contracted, and their walls less elastic. Hence the blood-pressure is high, the tidal wave large, and distinctly separated with well-marked dicrotic, and even a third secondary wave (Galabin).

3. The small hard pulse of peritonitis due to less vigorous action of the heart, with coincident contraction of smaller arteries.

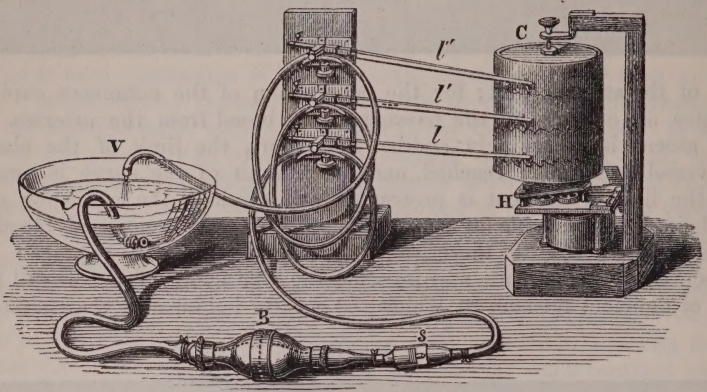
4. The small, soft, and thready pulse of collapse, in which the heart's action is feeble, and the vessels are relaxed with perhaps diminution of supply of blood.

5. The irregular and the intermittent pulse are conditions associated with disease of the heart and disordered cardiac innervation.

241. The mode in which the pulse is propagated through the arteries is made manifest by the following ingenious experiment devised by M. Marey:— A small caoutchouc bag (Fig. 139, B) is fitted with valves which permit the

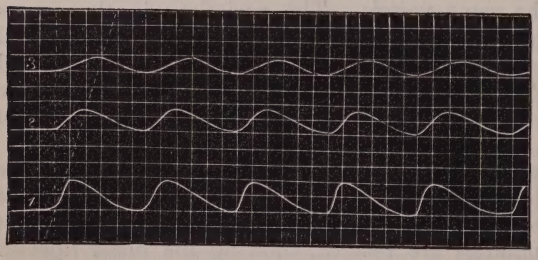
contained fluid to move only in one direction, and is connected with a long elastic tube forming a rude resemblance to the Heart and Arteries. At three different points of its length the tube is placed under the control of a Sphygmo-

Fig. 139.



graph, the levers of which, $l\ l'\ l''$, register their movements on the drum C in such a manner that their tracings may be exactly parallel and comparable with one another. Fig. 140 shows such a triple tracing after the india-rubber bag has been for a few times rhythmically compressed. It is here evident that, as indicated by the oblique dotted line, the period at which the maximum of tension is attained, is latest in that portion of the tube which is most distant from the impelling organ, and a certain, though minute, retardation occurs in the passage of the wave through the column of liquid. The actual amount of this retardation has been carefully investigated by Czermak,* with the aid of his photosphygmograph, in which the fluctuations of a ray of light reflected from a small mirror placed over the radial artery are registered on a screen of prepared photographic collodion. The mean of a series of twenty experiments showed that the pulse in the radial artery at the wrist was 0·18 sec. earlier than in the dorsal artery of the foot; whilst the shock of the heart, which is transmitted nearly instantaneously to all parts of the system, occurred 0·159 of a sec. earlier than the pulsation at the wrist, and 0·087 sec. earlier than the pulse in the carotid. It therefore takes about 1-6th of a second for the primary pulse wave to travel from the heart to the foot, and estimating this distance roughly at five feet, the rate of the pulse wave is about thirty feet a second, with which Weber's estimating (28·5 feet) closely agrees. The rate of the pulse wave is, of course, to be carefully distinguished from the velocity of the blood itself. Grunmach's experiments† show that in the healthy dog the rate of propagation of the pulse wave is 75 cm. in 0·158 sec. or 4·746 m. in one second

Fig. 140.



* "Mittheilungen aus dem Privat-Laboratorium," Heft 1, 1864, p. 27.
† "Archiv f. Anat. v. Physiol. His. and Braun.," 1879, p. 425.

(or about 15 feet). After paralysis of the peripheric vascular nerves by means of æther, chloral hydrate and morphin, the rate fell to 3·304 m. in one second, the blood pressure being coincidently reduced, and reduction to a still greater extent occurred after section of the spinal cord. On the contrary, when the blood pressure was increased by stimulation of the spinal cord, the rapidity of propagation of the pulse wave amounted to 6·25 m. in one second.

His experiments on man showed that the rapidity of propagation of the pulse wave was greater towards the lower extremity than along the arm, being, in one instance, 5·123 m. in one second along the arm and 6·620 m. towards the foot. It was smaller in children than in adults. As in the dog, circumstances that induced either local dilatation or local constriction of the lumina of the vessels caused retardation of the rate of propagation of the pulse wave. Again, in the above tracings it may be noticed that the force of the impulse, or the extent of the vertical movement of the lever, diminishes with increase of distance from the impelling organ, producing the effect which Poiseuille described as "extinction of the wave."

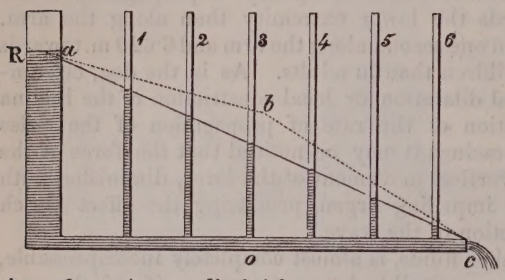
242. Since the blood, like other fluids, is almost completely incompressible, all force applied to it becomes perceptible by movement, or if this be prevented, by lateral pressure exerted against the sides of the vessels, and these two, the velocity of movement and the lateral pressure, however much each may vary in amount, always together represent the impelling force. The circumstances that chiefly affect the movement or velocity of the blood, independently of variations in the amount of the propelling force, are those which increase or diminish the friction between it and the vascular walls. Thus, it will be retarded by diminution of the diameter of the tubes, or, as was observed by Hunter, by curves, angles, or divisions in their course,* or by their rigidity,† or by increased viscidity of the blood itself; or, lastly, by augmentation, of its attraction for the tissues, or for the walls of the vessels through which it is coursing. These constitute the obstacles or resistance to the passage of the blood; and with their increase, if the impelling force remain the same, whilst the velocity of its movement is retarded, the amount of lateral pressure exerted is increased. The effects of diminished resistance in diminishing pressure may be understood from a consideration of Fig. 141. For here the height to which the fluid will rise in the small tubes numbered 1—6, is the expression of the pressure of the liquid against the walls of the tube R *o c* at different points. If the fluid were stationary, from the closure of the orifice *c*, it would, according to a well-known law, rise to the same height in all; but when a discharge is allowed to take place from *c*, a gradual diminution of pressure, indicated by the diagonal line R *c*, may be observed as the outlet is approached. Now, if the bore of the tube be contracted at any part, as at *o*, an obstacle to the discharge of the fluid will be created, through the increase of friction; the pressure against the walls of the preceding portion of the tube R to *o* will increase, and consequently the line of levels will rise in

* So Budge ("Physiologie," 1862, p. 309) found that a simple tube (*a*) would deliver more fluid in a given time than a bifid one (*b*), the sectional areas of whose arms were together equal to *a*, and the bifid tube more than a trifid one (*c*) in the proportion of (*a*) 3860 : (*b*) 3400 : (*c*) 3100, the pressure being equal in all three cases.

† Thus Marey has shown that whilst elastic and rigid tubes of equal diameters will discharge an equal quantity of fluid as long as the stream is continuous, the moment the stream becomes intermittent an advantage is gained by the elastic tubes, apparently owing to the diminution of friction in the latter, and the conversion of the jetting movement of the fluid into a more continuous, uniform, and steady flow; and herein, perhaps, we may perceive an explanation of the hypertrophy of the Heart, so frequently observed as a concomitant of a rigid aorta in old age. See "Annal. des Sci. Nat. Zool.," 1857, t. viii. p. 330; and Marey's "Thèse Inaugurale," 1859.

that part, as indicated by the dotted line R *b c*. If, on the other hand, the outlet be enlarged, the fluid will be discharged more easily, and the line of levels will fall with great rapidity. Upon these principles M. Marey* has constructed an apparatus bearing some resemblance to the different systems of vessels in the body, a constricted portion at *o* (Fig. 141) representing the capillaries,† and being preceded by a wider portion for the Arteries, and followed by a still wider one for the Veins. By this instrument it may be shown physically that the pressure is highest in the Arterial vessels, whilst it is much less in the Capillaries, and is lowest in the Veins.‡ It may also be shown that the mean tension of an Artery diminishes in proportion to its distance from the heart, and is by so much the less in proportion as the capillaries are dilated, and thus constitute a smaller obstacle to the passage of the arterial blood. These facts, at least as regards the difference of the pressure in the arterial and venous systems, were clearly perceived by Hales, and having been substantiated by Bernard with the differential Manometer, Fig. 142 ; the two mouthpieces of which, *e e*, being inserted into Arteries at the same distance from the heart, as the two carotids or the two crurals, the level of the mercury on the two sides remains equal, indicating equality of pressure; whilst if one be placed in a more distant Artery or into a Vein, the mercury constantly rises on that side, thus showing a diminution of pressure or tension. If the contracted or capillary portion of Marey's apparatus be enlarged, the fluid will pass through it with less resistance, and the pressure in the Arterial portion will diminish, and *vice versâ*. This has actually been observed by Bernard in the living subject: for on placing the mouthpieces of his differential Manometer into the two facial arteries of a horse, the mercury stood at the same level in each arm of the instrument; but on division of one of the cervical sympathetic nerves, the mercury instantly rose on that side, indicating a diminution in the tension of the vessel. Now it has been ascertained by M. Brown-Séquard that section of the sympathetic causes a dilatation of the Capillary vessels, and therefore facilitates the passage of the blood through them; and the counter-proof is shown by stimulating the cut extremity of the Sympathetic, which inducing contraction of the Capillaries, increases the resistance to the passage of the blood from the arteries, and augments the tension of their walls, as is indicated by the gradual falling of the mercury on the stimulated side, till the pressure there may even exceed that of the healthy one.

Fig. 141.



243. The absolute pressure of the blood in the living vessels has engaged the attention of many observers. Hales§ endeavoured to ascertain it by inserting long pipes into the vessels of living animals, and measuring the

* Brown-Séquard's "Journ. de la Physiol.," vol. ii. p. 436. See also Rutherford's 'New Scheme of the Circulation,' "Journ. of Anat. and Phys.," 1872, vol. vi. p. 249.

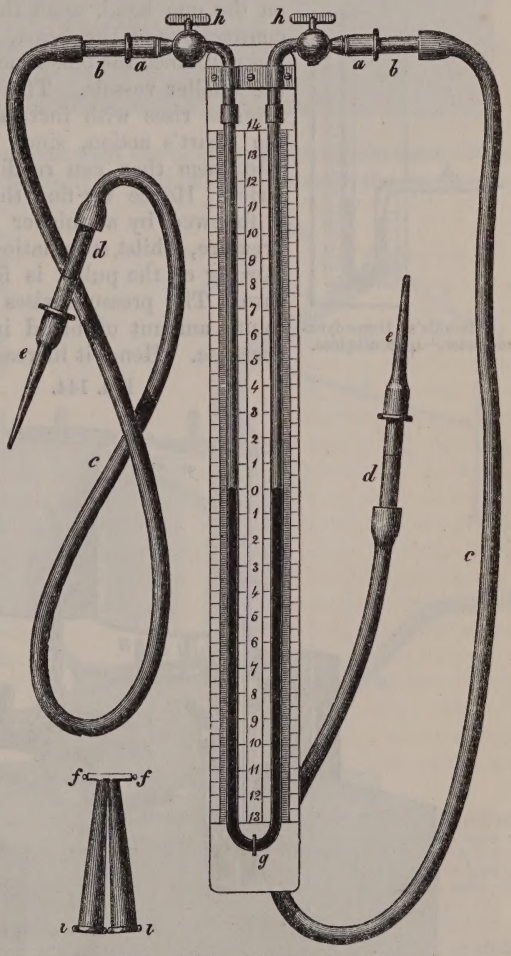
† The capillaries of the body, though in their aggregate sectional area much larger than the aorta, yet by reason of their smallness, and the consequent great increase of friction against their walls, operate virtually as such a constricted portion.

‡ In the living body the pressure rises again in the veins, as their collective calibre is much less than that of the capillaries, though greater than that of the arteries.

§ "Hæmastatics," vol. i. pp. 1–60.

height to which the blood rose. In a Mare, when the tube was introduced into the crural artery, it rose 8 ft. 3 in.; in two Horses, 9 ft. 8 in. and 9 ft. 6 in. From parallel experiments upon sheep, oxen, dogs, and other animals, and from the comparison of the calibre of their respective vessels with that of the human aorta, Hales concluded that the usual force of the heart in man would sustain a column of blood 7½ ft. high, the weight of which would be about 4 lbs. 6 ozs. on the square inch. Poiseuille, improving on Hales' method, employed a much more portable instrument in the form of a doubly-bent tube (Fig. 143), containing mercury in the curve, and a solution of carbonate of soda in the mouthpiece, which prevented the formation of clots. A still further improvement was made by Ludwig and Volkmann, by placing Poiseuille's instrument in connection with a revolving drum, on which tracings indicating the fluctuations of the pressure could be taken. The instrument so modified is called the "Kymographion," and is represented in Fig. 144. The tracing on page 321 gives a normal tracing of arterial pressure obtained with the mercurial Kymograph from a rabbit. Poiseuille estimated the pressure in the arteries at 6·3 inches of mercury on the square inch, which he assumed as the standard for all arteries, and for all Mammalia. But the tracings of Ludwig and Volkmann showed that the range of variation is very wide, being in the carotid of the Horse from 6–13 inches, in the Dog from 7–8 inches, and in the Rabbit from 2–3½ inches; in Man it is probably about equal in the larger arteries to a column of mercury 8 inches in height (Ranke, 6 or 7 Faivre). Bernard has invented a lighter instrument, termed the "Cardiometer," the indications given by which are somewhat higher than those obtained by Poiseuille's apparatus. The following table presents the results of Volkmann's observations† upon the relative lateral pressure at four points of the circulation in different animals, expressed in millimetres—namely,

FIG. 142.



Differential Manometer of Bernard.*

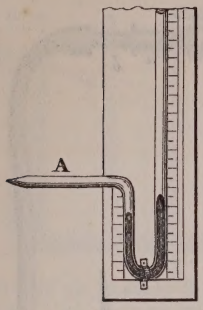
* Bernard, vol. i. p. 205, 1859.

† Op. cit., p. 173.

(I.) the carotid near its origin, (II.) a peripheral branch of the carotid or some other artery, (III.) a peripheral rootlet of a vein, and (IV.) a jugular vein :—

	I.	II.	III.	IV.
Goat . . .	135	126	41	18 mm.
Horse . . .	122	97	44·5	21·5 mm.
Calf . . .	165·5	146	27	9 mm.

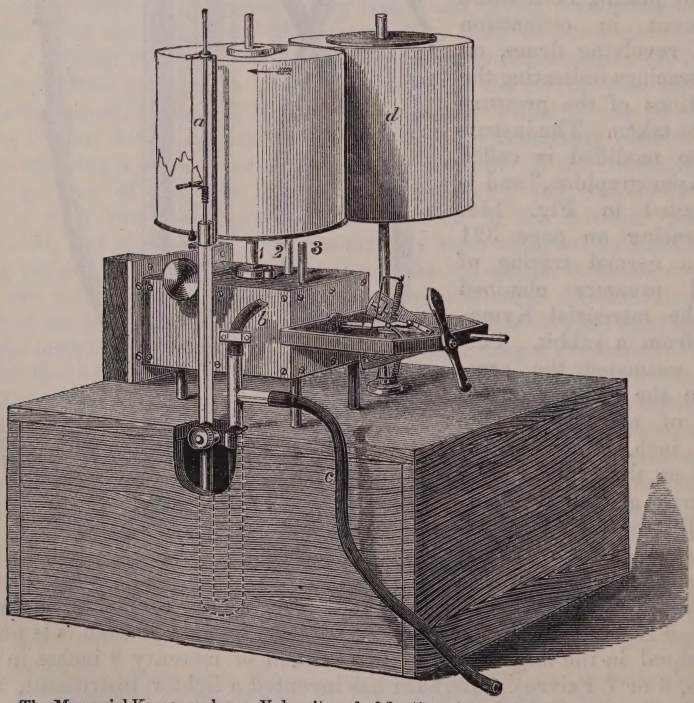
Fig. 143.



Poiseuille's Hæmadynamometer.—A, mouthpiece.

The periodic variations of the blood-pressure depend, on the one hand, upon the frequency and vigour of the contractions of the heart, and, upon the other hand, on the resistance the blood meets with in its passage through the smaller vessels. The pressure of the blood in the arteries rises with increased strength and frequency of the heart's action, since more blood is then pumped into them than can readily escape through the capillaries. Hence we find that section of the vagus which is followed by a quicker pulse, produces higher mean pressure, whilst stimulation of the vagus, which causes slowing of the pulse, is followed by a fall in the pressure. The pressure rises with any increase in the absolute amount of blood in the system, and falls with a decrease. Hence it increases after meals, and diminishes

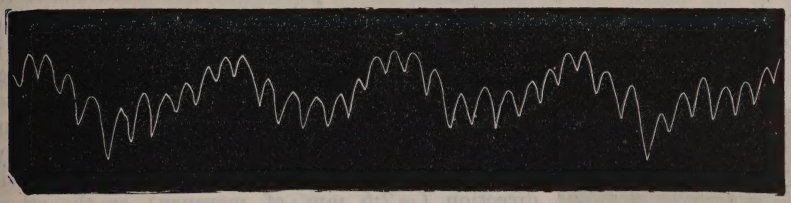
Fig. 144.



The Mercurial Kymograph.—*a*, Vulcanite rod of floating piston ; *b*, tube which communicates with the pressure-bottle ; *c*, tube which communicates with the artery ; *d*, feeding cylinder. 1. First axis, which revolves once in a minute ; 2, second axis, which revolves once in ten seconds ; 3, axis, which revolves in 1½ seconds. The instrument is furnished with other cylinders suitable for the reception of bands of paper, the surface of which can be blackened after they are fixed on to the cylinders, by causing the cylinder to revolve over the flame of a petroleum lamp, though more frequently the tracings are taken with a brush wetted with solution of anilin dye.

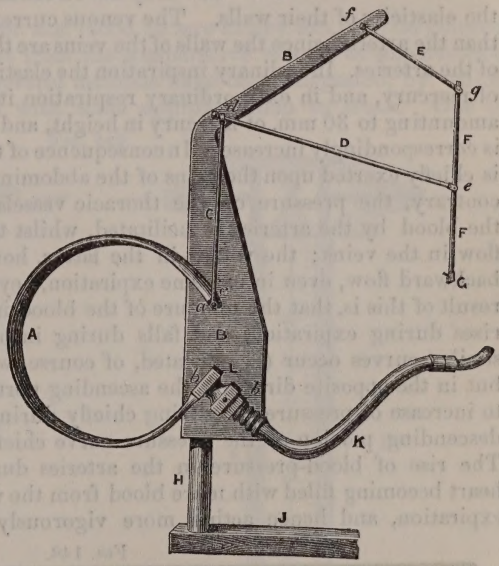
after fasting. The pressure rises when, from any cause, the smaller vessels contract, since this must increase the resistance to the discharge of the blood from them;

Fig. 145.



and it falls when they dilate, because then the blood traverses them more easily. Hence it rises on exposure of the body to cold, which contracts the capillaries, and falls in a warm temperature, which leads to the dilatation of the capillaries, and this shows too that local variations in the contraction of the vessels influence the pressure of the blood in the rest of the system. Constriction of a particular artery causes diminished flow through the artery itself, increase of the pressure of the blood throughout the arterial system, and augmentation of the flow of blood through all the other arteries of the body; whilst dilatation of an artery has the opposite effect. Fick,* from experiments made on the dog with his modified spring manometer (Fig. 146), found the pressure in the right auricle nil (= atmospheric pressure); during inspiration it sank to 10 mm. of mercury below zero. In the right ventricle the pressure varied from 18–42 mm., and in the left ventricle the maximum was 140 mm. The pressure of the blood in the aorta rose as high during the period of systole as in the ventricle, but it did not fall so low during the diastole. Badoud,† working under Fick and using his C-spring manometer, found the pressure of the blood in the pulmonary artery constantly below 60 mm. of mercury; after section of the spinal cord it fell considerably, and when the cord was stimulated electrically it not only rose, as occurs in the systemic arteries, but rose considerably above the normal, this being due to the muscular contraction excited in the body generally. Worm Müller‡ has shown that when the tension of the vascular system has been lowered by section of the spinal

Fig. 146.

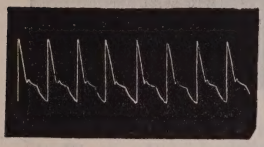


Fick's Spring Kymograph.—A, C-spring; B B, support; C, rod which communicates the movements of the spring to the lever D, and thus to the writing-needle G, the verticality of the movement of which is secured by the second rod E; K, leaden tube by which the cavity of the spring is in communication with the artery.

* "Verhand. d. Wurzburg Phys.-Med. Ges.," Band iv. 1873, p. 223.
† "Inaug. Dissert.," Wurzburg, 1874. ‡ "Sitz.-ber. d. Sächs. Ges. d. Wiss.," 1873, p. 573.

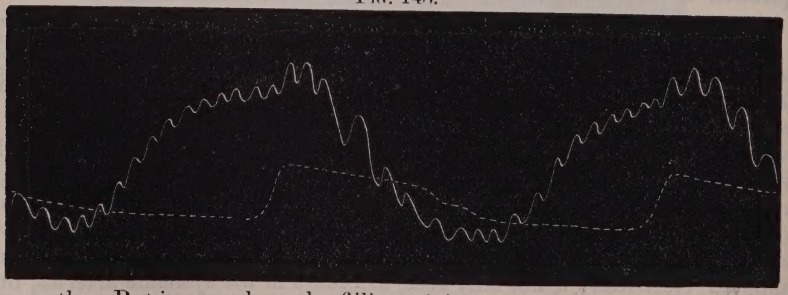
cord and cardiac nerves, the blood-pressure cannot again be raised to its normal height by the injection of blood into the vessels. He also showed that blood to the extent of two per cent. of the body weight can be withdrawn from the body without materially lowering the blood-pressure. The influence of the respiratory movements upon the pressure of the blood in the vessels is of much interest.* After an ordinary expiration the heart and large vessels in the chest are exposed to a pressure acting through the tissue of the lung, which, as Wündt has pointed out, is equal to the difference between the pressure of the air on the one hand (=750 mm. of mercury) and the elasticity of the lungs acting in the opposite direction (=7·5 mm. of mercury) on the other; whilst on the vessels outside the full pressure of the air is exerted. The blood cavities in the chest being thus exposed to less pressure than those of the rest of the body have a tendency to dilate until restrained by the elasticity of their walls. The venous current is affected to a greater degree than the arterial, since the walls of the veins are thinner and less elastic than those of the arteries. In ordinary inspiration the elasticity of the lungs rises to 9·5 mm. of mercury, and in extraordinary respiration it would even support a column amounting to 30 mm. of mercury in height, and the suction power of the cavities is correspondingly increased. In consequence of the descent of the diaphragm this is chiefly exerted upon the veins of the abdominal viscera. In expiration, on the contrary, the pressure on the thoracic vessels being increased, the escape of the blood by the arteries is facilitated, whilst there is a tendency to arrest the flow in the veins; the valves in the latter, however, offer an obstruction to a backward flow, even in extreme expiration, beyond certain limits. The general result of this is, that the pressure of the blood in the veins of the body at large, rises during expiration, and falls during inspiration. In the arterial tracing similar curves occur (complicated, of course, with those of the cardiac beats), but in the opposite direction, the ascending portion of the curve (corresponding to increase of pressure) occurring chiefly during the period of inspiration, the descending portion of the pressure-curve chiefly occurring during expiration. The rise of blood-pressure in the arteries during inspiration depends on the heart becoming filled with more blood from the veins at this period than during expiration, and hence acting more vigorously and at the same time more

Fig. 147.



Normal arterial tracing obtained with the Spring Kymograph; dog under Curare.

Fig. 148.



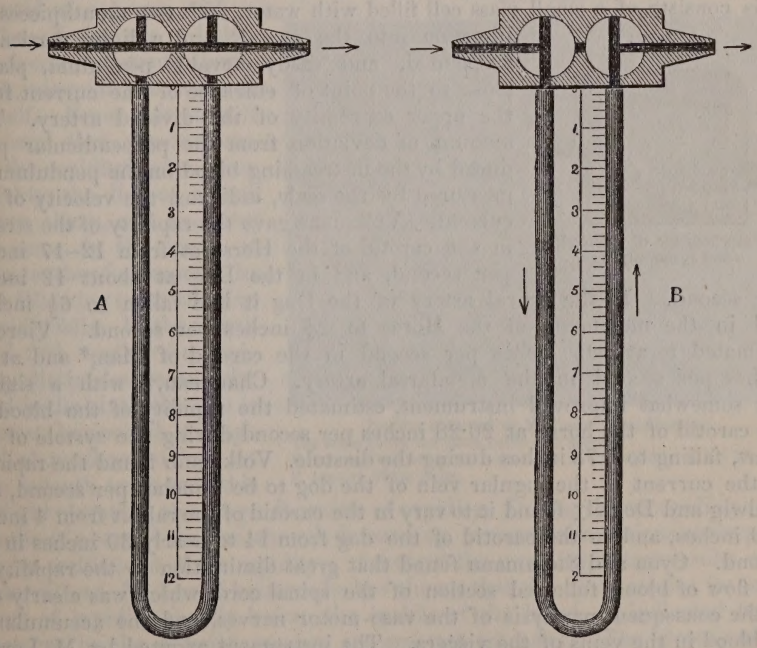
frequently. But inasmuch as the filling of the cardiac cavities with blood does not take place at the commencement of inspiration, nor the diminished supply of blood to them with the commencement of expiration, and since, further, the dimi-

* See Zuntz, Pflüger's "Archiv," Band xvii. 1878, p. 374; also Funke and Latschenberger, idem., p. 547.

nution of pressure within the thoracic cavity in expiration exerts a suctional power upon the contents of the arteries, whilst the increase of pressure during expiration tends to drive out the blood, it comes to pass, as was shown by Einbrodt,* that the respiratory phases represented by the dotted line in the accompanying figure (Fig. 148) do not exactly correspond with the variations of pressure, but that the pressure continues to fall for a little while after the commencement of inspiration, and continues to rise for a little while after the commencement of expiration. Curves essentially similar to those observed in normal respiration are seen when the animal is poisoned by curare, if artificial respiration be maintained. On suspending the artificial respiration the mean pressure rises, and curves (Traube's curves) then begin to appear, which gradually become more and more marked, and are synchronous with the suppressed respirations; they are probably partly dependent on the relation of the gases in the blood to the vaso-motor centre, and partly to the direct action of the imperfectly arterialized blood upon the local nerve centres of the vessels themselves.

244. *The rate of movement* of the blood in any artery can only be guessed at as regards the human subject from the comparative results of experiments upon the lower animals; but several methods have been suggested, by which it may be ascertained in them with some approximation to truth. One of

Fig. 149.



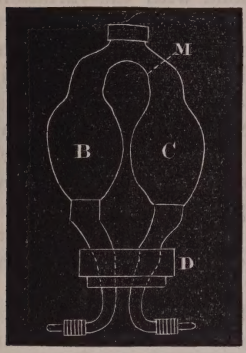
Volkmann's Hæmodromometer.

these, employed by Volkmann, and termed by him the Hæmodromometer, is exhibited in Fig. 149, where A shows the instrument as it is inserted between the two cut extremities of an artery or vein. In this position the blood continues to flow in the original direction; but by a simple mechanical arrange-

* "Sitz.-ber. d. k. Akad. zu Wien.," 1859, p. 345. See also Funke, "Physiologie," Band i. 1863, p. 135; Wundt, "Physiologie," 1873, p. 314; Sanderson, in "Handbook for the Physiological Laboratory," 1873, p. 314.

ment its course can be suddenly diverted (as in B), through the bent tube filled with serum in the direction of the arrows. The rapidity of the current may be readily estimated by timing its course along the scale at the side.

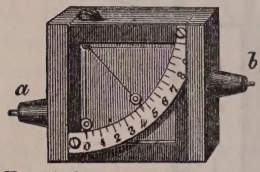
Fig. 150.



Ludwig's Stromuhr.

Ludwig has suggested an instrument which he has named a "Stromuhr," or current measurer, the principle of which is represented in Fig. 150. This consists of an arched glass vessel with two legs, of which B and C are considerably dilated, and the extremities of which are inserted into the vessels; that directed towards the heart, C, being filled with pure olive oil, whilst the other directed towards the capillaries is filled with defibrinated blood. If the capacity of the limb C up to the point M be known, and the time occupied in filling it be noted, it is easy to calculate the quantity of blood passing through the artery in a given period. At D is a mechanical arrangement by which the current of blood through the two limbs may be reversed, and the experiment repeated on the same animal. A third instrument, adapted for measuring the rapidity of the blood-current is that represented in Fig. 151, devised by Vierordt, and termed by him the "Hæmatochometer." This consists of a small glass cell filled with water, with two mouthpieces for insertion into the vessel, and a light vertically-suspended, and easily-movable pendulum, placed close to the point of entrance of the current from the upper extremity of the divided artery. The amount of deviation from the perpendicular produced by the instreaming blood on the pendulum, as measured by the scale, indicates the velocity of the current. Volkmann gave the rapidity of the stream in the carotid of the Horse at from 12–17 inches per second, and in the Dog at about 12 inches per second. In the crural artery of the Dog it had fallen to $6\frac{1}{2}$ inches, and in the metatarsal of the Horse to $2\frac{1}{4}$ inches per second. Vierordt estimated it at $10\frac{1}{2}$ inches per second in the carotid of Man,* and at $2\frac{1}{4}$ inches per second in the metatarsal artery. Chauveau,† with a similar but somewhat improved instrument, estimated the rapidity of the blood in the carotid of the horse at 20·28 inches per second during the systole of the heart, falling to 8·78 inches during the diastole. Volkmann found the rapidity of the current in the jugular vein of the dog to be 9 inches per second, and Ludwig and Dogiel‡ found it to vary in the carotid of the rabbit from 4 inches to 9 inches, and in the carotid of the dog from 14 to nearly 30 inches in the second. Cyon and Steinmann found that great diminution in the rapidity of the flow of blood followed section of the spinal cord, which was clearly due to the consequent paralysis of the vaso-motor nerves, and the accumulation of blood in the veins of the viscera. The instrument adopted by M. Lortet§

Fig. 151.



Hæmatochometer of Vierordt.—*a* and *b*, mouthpieces.

* "Physiologie," p. 110, 1861.

† "Archiv. Gén. de Méd.," vol. i. 1861, p. 113; and "Jour. de la Phys.," 1860, p. 695.

‡ Ludwig's "Arbeiten," 1867, p. 196. See also 'Notes on some Experiments on the Rate of Flow of Blood, and some other Liquids, through Tubes of Narrow Diameter,' by Drs. Duncan and Gamgee, "Journ. of Anat. and Phys.," vol. v. 1871, p. 150; and Cyon and Steinmann, "Bull. de l'Acad. Impériale de St. Pétersbourg," t. viii. p. 55.

§ "Recherches sur la Vitesse du Cours du Sang," &c., Paris, 1868.

(Fig. 152) is founded on the same principle as the one suggested by MM. Chauveau, Bertolus, and Laroyenne.* It consists of a short tube, open at both ends (*a*), which is introduced into the artery. On one side, near the middle, is a square opening (*b*), which is closed by a plate of caoutchouc. The caoutchouc is pierced by a long and light lever (*c*), the short and somewhat broader end of which hangs in the current of blood, whilst the long end records its corresponding but opposite movements on a rotating drum, the fulcrum being the point where the lever is gripped by the sides of the opening in the india-rubber. Connected with the instrument is a sphygmoscope and a sphygmographic apparatus, with the object of obtaining traces of the pulsations, the tube of the former being soldered, on the one hand, into the side of the primary or hæmodromographic tube, and, on the other, being connected with an elastic cushion filled with air and supporting a lever the movements of which are registered just below those of the lever indicating the rapidity of the movement of the blood. Fig. 153 shows a double normal tracing obtained from the carotid of a horse with a pulse of 40 per minute. Each complete trace, therefore, occupied a second and a half. From this it will be seen that the increase of the rapidity commences briskly, the line of ascent being sharp, and reaching its acme in the space of two-tenths of a second. In the following tenth the line rapidly falls. In the fourth and fifth tenths the rapidity diminishes insensibly, and in the sixth the line is almost horizontal, though still above the zero line. At the seventh-tenth second is a slight elevation, showing a dicrotism of rapidity. During the succeeding eight-tenths of a second the line, though descending, presents undulations corresponding to oscillations of the rapidity. Amongst the more important results of his observations, M. Lortet believes he has shown that the blood attains its maximum of rapidity shortly before the systole of the heart, as indicated by the pressure in the arteries, reaches its greatest intensity. The closure of the sigmoid valves exerts little influence on the rapidity. The rapidity is greatest during expiration, and least during inspiration. Section of the spinal cord in the atlo-occipital region, or of the Pneumogastrics, increases both the speed of the blood and the pressure in the arteries. On ligature of one carotid the rapidity of the blood was found to increase in the other.

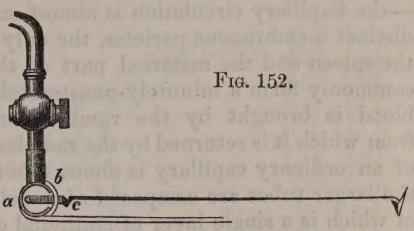
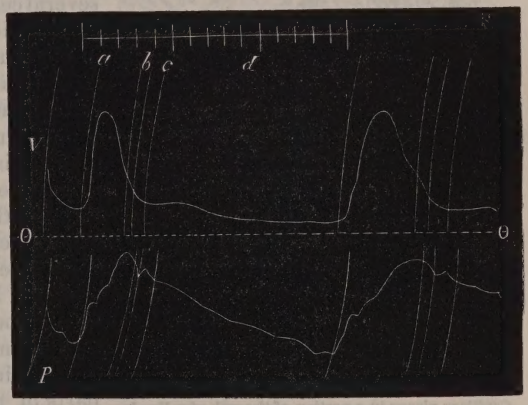


Fig. 152.

M. Lortet's Instrument.

Fig. 153.



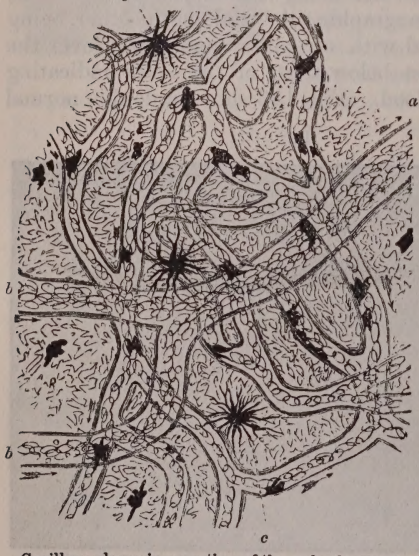
Tracing obtained by M. Lortet's Instrument.
The scale above indicates 10ths of a second.
V, tracing indicating the variations in the rapidity of the blood.
P, tracing of the pulse.

* "Journal de la Physiologie," Brown-Séquard, 1860, t. iii.

4. *Movement of the Blood in the Capillaries.*

245. In Man, as in all the higher Animals—in the adult condition at least—the Capillary circulation is almost entirely carried on through tubes having distinct membranous parietes, the only known exceptions being in the case of the spleen and the maternal part of the placenta (§ 157, II.)* These tubes commonly form a minutely-anastomosing network (Fig. 154), into which the blood is brought by the ramifications of the arteries on one side, and from which it is returned by the radicles of the veins on the other. The length of an ordinary capillary is about 1-50th to 1-25th of an inch. The walls of the larger tubes are composed of a delicate membrane, on the inner surface of which is a single layer of epithelial cells possessing nuclei, and of fusiform shape, in this respect resembling the cells lining the smaller arteries, but differing from those in the interior of the veins, which are lozenge-shaped, with wavy outline (Fig. 155). The walls of the very finest capillaries, as those of the retina and brain, are composed of a single layer of nucleated cell plates intimately united by an albuminous interstitial cell substance which is readily stained with nitrate of silver. The several cells are elongated, have pointed extremities, and are smooth or sinuous in contour (Fig. 155). They contain an intra-nuclear plexus of fibrils (Klein), and an oval flat nucleus. When the emigration of white corpuscles or diapedesis of red corpuscles is taking place, the corpuscles make their way through the cement substance, and this occurs especially in inflammation, when the capillaries are greatly distended. Minute openings or stigmata then appear which may enlarge till they form stomata. The capillaries in certain regions,† as the central parts of the nervous system and the mesentery, appear to be surrounded by a sheath between which and their own proper coat, lymph corpuscles have been observed; these spaces have consequently been regarded as extensions of the lymphatic system. Frey remarks, however, that it is not every adventitial tissue of a blood-vessel containing lymphoid cells that must be regarded as a lymph sheath. A circumstance that may frequently give rise to the deceptive appearance of such a sheath is that a blood-vessel is often bounded on each side by lymphatic canals, and this is most commonly seen in uninjected preparations. Without any basement membrane, this last only becoming perceptible in those of larger

Fig. 154.



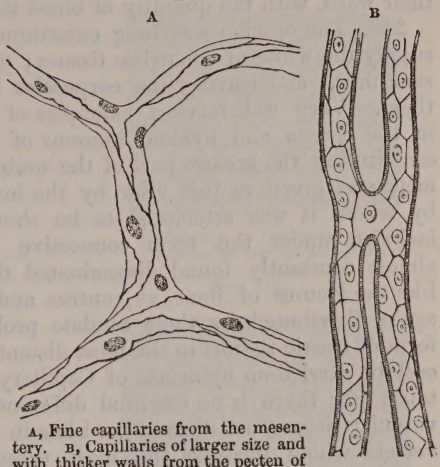
Capillary plexus in a portion of the web of a *Frog's* foot, magnified 110 diameters.—*a*, trunk of vein; *b*, *b*, its branches; *c*, *c*, pigment cells.

* The capillary circulation may be well seen in the web of the foot, in the lung, mesentery, and tongue of the frog, the tail of tadpoles and of fish (see Caton, "Quart. Journ. of Mic. Science," 1870, p. 236), and in the peritoneum of mammals by the plan suggested by Stricker and Burdon-Sanderson, in which a guinea-pig is chloralized, the abdominal cavity opened, and the omentum floated in a warm bath containing common salt in solution. (See "Quart. Journ. of Mic. Science," Oct. 1870.)

† Stricker, in Moleschott's "Untersuch.," Band x. Heft 2, p. 168.

diameter.* Non-medullated nerve-fibres have been traced by Beale to the capillaries, and by the aid of the gold method of staining, Klein has followed still finer fibres into the substance of the capillary wall.† The diameter of the capillaries varies in different parts of the body; those of the brain and lung being smaller than those of the liver or of bone. It also differs in different animals, in accordance with that of their blood-corpuscles; thus, the capillaries of the frog are, of course, much larger than those of Man. The ordinary diameter of the latter appears, from the measurements of Weber, Müller, and others, to vary from about the 1-300th to the 1-2500th of an inch; the extremes, however, are stated by Kölliker at as little as 1-5600th and as much as 1-1870th of an inch. As the diameter of the human capillaries, however, can only be examined after death, it is probable that these statements may not be altogether correct, particularly as tubes of the smallest of the above sizes would not admit ordinary blood-corpuscles. The dimensions of the individual vessels, indeed, are by no means constant; as may be seen by watching the circulation in any transparent part, for some little time. Putting aside those general changes in diameter which result from circumstances affecting all the capillaries of a part, it may be observed that a single capillary will sometimes enlarge or diminish by itself, without any obvious cause. Thus, the stream of blood will sometimes be seen to run into passages which were not before perceived; and it has hence been supposed that they were new excavations, formed by the retreating or removal of the solid tissue through which it passes. But a more attentive examination shows that such passages are real capillaries, which did not at the time of the first observation admit the stream of blood-corpuscles, in consequence of their small calibre, or of some other local impediment; and that they are brought into view by the simple increase in their diameter. The compression of one of the small arteries will generally occasion an oscillation of the corpuscles of blood in the smallest capillaries, which will be followed by the disappearance of some of them; but when the obstruction is removed, the blood soon regains its previous velocity and force, and flows into exactly the same passages as before. The capillaries of the red muscles of rabbits exhibit dilatations or small aneurismal enlargements, which may be regarded as constituting reservoirs

Fig. 155.



A, Fine capillaries from the mesentery. B, Capillaries of larger size and with thicker walls from the pecten of the eye of abird.

* Eberth, "Wurzburg. Naturwiss. Zeit.," Band vi. 1865, p. 27, and Stricker's "Hum. and Comp. Histology," Syd. Soc. Trans., Art. 'Bloodvessels.' See also Chrzonszczewsky, Virchow's "Archiv," 1866, Band xxxv. p. 171; Auerbach, "Breslau. Zeitung," 1865; Aeby, "Medicin. Centralblatt," 1865, No. 14; Cohnheim, Virchow's "Archiv," Band xv. p. 52, and Ranvier and Cornil in Brown-Séquard's "Archiv. de Physiol.," t. i. 1868, p. 551; Klein and Noble's, "Atlas," p. 137.

† Klein, 'Distribution of Non-medullated Nerve-fibres,' "Quart. Journ. of Mic. Sci.," 1872, p. 125. An appendix to this paper contains a list of thirty-eight memoirs on this subject. Beale, 'The Nerves of Capillary Vessels,' &c., "Monthly Microscop. Journ.," 1872, vol. viii. p. 57.

or storehouses of oxygenated blood for the supply of the muscles during their contraction.* It is still doubtful whether the capillaries possess any contractile power of their own, or merely vary in size owing to the elasticity of their walls, with the quantity of blood they contain.†

246. The opinion was long entertained that there are vessels adapted to supply the white or colourless tissues; carrying from the arteries the 'liquor sanguinis,' and leaving the corpuscles behind, through inability to receive them. Very well-marked examples of such non-vascular tissues are found in the cornea and hyaloid humour of the eye, and in the mucous tissue constituting the greater part of the umbilical cord. A considerable development was given to this view by the investigations of Virchow‡ and others; by whom it was attempted to be shown that in the various structures included under the term connective tissues, the corpuscles, which are almost constantly found disseminated through them, are to be regarded, like the lacunæ of bone, as centres and storehouses of nutriment, which is again distributed by their caudate prolongations (frequently assuming the form of elastic tissue) to the most distant parts. The idea that Nutrition can *only* be carried-on by means of Capillary vessels is, however, entirely gratuitous; for there is no essential difference between the nutrition of the non-vascular tissues, and that of the islets in the midst of the network of capillary vessels which traverse the most vascular. In both cases, the nutrient materials conveyed by the blood are absorbed by the cells or other elementary parts of the tissue immediately adjoining the vessels, and are imparted by them to others which are further removed; and the only difference lies in the amount of the portion of tissue which has to be thus traversed, so that we are only required to extend our ideas, from the largest of the islets which we find in the vascular tissues, to the still more isolated structures of which the non-vascular tissues are composed.—The disposition of the Capillaries, both as to the degree of minuteness and the plan of the reticulation which they form, varies so greatly in the different vascular tissues that it is possible to state with tolerable certainty the nature of the part from which any specimen has been detached,—whether a portion of Skin (Fig. 156), Mucous membrane (Fig. 157), Serous membrane, Muscles (Fig. 158), Nerve, Fat (159), Areolar tissue, Gland, &c. The degree of minuteness is obviously in accordance with the copiousness of the supply of blood which is required for the purposes of its circulation through the part; thus, the plexus is closest, where some change is to be effected in the blood itself, as in the absorbent, respiratory, and secreting organs; whilst it is widest in those parts which receive the blood solely for their own nutrition,—the nervous centres and muscles having a more minute reticulation than is seen in the generality of the last-named parts, in virtue of the peculiar activity of the molecular changes which take place in them. But the arrangement of vessels peculiar to each, evidently has reference only to the convenience of the distribution of blood among the elementary parts of the tissue, and varies with their form. It is not possible to imagine that it has any other relation than this to their functions; since the function of each separate element of the organ, of which that of the entire organ is the aggregate, is due to its own inherent vital

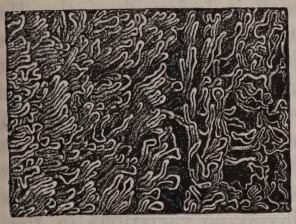
* Ranvier, "Archiv. de Physiologie," 1874, t. i. Peremeschkow, however, has observed similar enlargements in the capillaries of the ligamentum nuchæ of the dog and cat. Carus' "Zoolog. Anzeiger," 1878, p. 200.

† See Eberth, op. cit., and Stricker, "Wien. Sitz.-berichte," Band li. and liii. for arguments in favour of the former view, which are vigorously contested by Beale, op. cit., and Vulpian, "Leçons sur l'Appareil Vaso-moteur," 1875, p. 73.

‡ See "Cellular Pathology," *passim.*

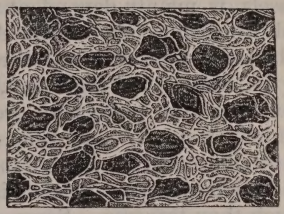
powers,—the supply of blood being only required as furnishing the material on which these are to be exercised.

Fig. 156.



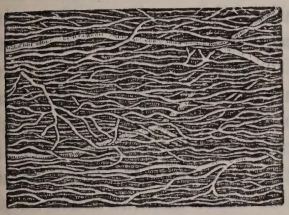
Distribution of *Capillaries* on the surface of the *Skin* of the finger.

Fig. 157.



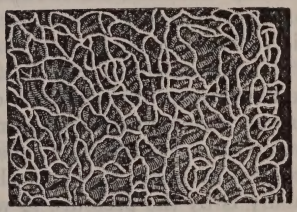
Distribution of *Capillaries* around follicles of *Mucous Membrane*.

Fig. 158.



Distribution of *Capillaries, in Muscle*.

Fig. 159.



Capillary network around *Fat-cells*.

247. The average *rate of movement* of the blood through the Capillary system may be determined with tolerable precision by microscopic measurement; and the observations of Hales, Valentin, and Weber concur in representing it to average in the systemic capillaries of the Frog 1·2 inch per minute.* In warm-blooded animals, however, the capillary circulation is probably much more rapid than this; the observations of Volkmann upon the mesenteric arteries of the Dog making its rate about 1·8 inch per minute; whilst Ludwig and Vierordt, from observations on the movement of the blood-corpuscles in the retinal capillaries of their own eyes, estimate the rapidity at from one inch in 41 seconds to one inch in 28 seconds. The layer which is in immediate proximity to the wall of the vessels flows from 9 to 17 times more slowly if the movement of the white corpuscles is to be taken as a means of estimating it (Weber). Assuming ·03 inch per second, however, as the rate, and comparing this with the rate of movement of the blood in the larger arteries, which seems on the average to be 11·8 inches per second, it is calculated by Volkmann that the aggregate area of the capillaries (being in an inverse ratio to the rate of the blood's movement through them) must be nearly *four hundred* times that of the arterial trunks which supply them.† Donders, on similar data, estimates it at 500 times greater, and Vierordt at from 800 to 850 times.‡ In regard to the pressure of the blood in the capil-

* Mosso, "Jahresber," 1874, vol. ii. p. 46; and Haro, idem., 1876, vol. ii. p. 79; Ewald, "Archiv f. Anat. u. Phys.," 1877, p. 208. The time occupied in the passage, or, as it is termed, the "transpiration-period" of the blood of the dog, through capillary tubes as compared to water taken as unity is 0·27, whilst human blood flows more rapidly, the proportion being 1 : 0·41. It runs more slowly as the temperature increases, and it also increases with increased specific gravity of the blood. The addition of carbonic acid gas, nicotin, chloral, ether, and small quantities of glycocholate of soda, retarded the passage; freezing and thawing again augmented it. See also Matthews Duncan and A. Gamgee, "Journ. of Anat. and Physiol.," vol. v. 1871, p. 150.

† "Hämodynamik," pp. 184, 204.

‡ "Die Erscheinungen und Gesetze der Stromgeschwindigkeit des Blutes," 1858.

laries, Kries* finds the average amount in those of the tips of the fingers equal to a column of 37·7 mm. of mercury or 513 mm. of water.

248. That the movement of the blood through the Capillary system of vessels is mainly dependent upon the force which it derives from the Heart and from the coats of the Arteries, is a matter altogether beyond dispute. When the flow of blood through the capillaries of a transparent part, such as the web of a Frog's foot, is observed with the microscope, it appears at first to take place with great evenness and regularity. But on watching the movement for some time, various changes may be observed, which cannot be attributed to the heart's influence, and which show that a certain regulating or distributive power exists in the walls of the capillaries, or in the tissues which they traverse. Some of these changes, involving variations in the *size* of the capillary tubes, have been already referred to (§ 245), Others, however, are manifested in great and sudden alterations in the velocity of the current, which cause a marked difference in the rates of the movement of the blood through the several parts of the area under observation. Sometimes this variation extends even to the entire reversal, for a time, of the direction of the movement, in certain of the transverse or communicating branches; the flow always taking place, of course, from the stronger towards the weaker current. Not unfrequently an entire stagnation of the current in some particular tube precedes this reversal of its direction. Irregularities of this kind, however, are more frequent when the heart's action is partly interrupted; as it usually is by the pressure to which the tadpole or other animal must be subjected, in order to allow microscopic observations to be made upon its circulation. Under such circumstances, the varieties in the capillary circulation, induced by causes purely local, become very conspicuous; for when the whole current is nearly stagnated, and a fresh impulse from the heart renews it, the movement is not by any means uniform (as it might have been expected to be) through the whole plexus supplied by one arterial trunk, but is much greater in some of the tubes than it is in others; the variation being in no degree connected with their size, and being very different at short intervals.

249. Cases are of no very unfrequent occurrence in which the heart is absent during the whole of embryonic life, and yet the greater part of the organs are well developed. In most or all of these cases, it is true, a perfect twin fœtus exists, of which the placenta is in some degree united with that of the imperfect one; and it has been customary to attribute the circulation in the latter to the influence of the heart of the former, propagated through the placental vessels. This supposition had not been disproved (however improbable it might seem), until a case of this kind occurred, which was submitted to the most careful examination by an accomplished anatomist;† when the decisive result was obtained, that it seemed impossible for the heart of the twin fœtus to have occasioned the movement of blood in the imperfect one, and that some cause present in the latter must have been sufficient for the propulsion of blood through its vessels. It was a very curious anomaly in this case, that the usual functions of the arteries and veins must have been reversed; for the Vena Cava, receiving its blood from the umbilical vein nearly as usual, had no communication with the Arterial system (the Heart being absent), except

* Ludwig's "Arbeiten," 1875, p. 69, and "Uber. den Druck in den Blut-Capillaren der Menschlichen Haut." in the "Ber. de Konig. Sachs. Ges. d. Wiss. zu Leipzig," vol. i. 1875, p. 149.

† See Dr. Houston in the "Dublin Medical Journal," 1837.—An attempt was made by Dr. M. Hall ("Edinb. Monthly Journal," 1843) to disprove Dr. Houston's inferences; but a most satisfactory reply was given by Dr. Houston, at the meeting of the British Association, August, 1843, and published in the "Dublin Journal," Jan. 1844. See also "Edin. Med. and Surg. Journ.," July, 1844.

hrough the systemic capillaries; to which, therefore, the blood must have ext proceeded, returning to the placenta by the umbilical artery. This view f the course of the blood was confirmed by the fact that the veins were every- where destitute of valves.—It is evident that a single case of this kind, if nequivocally demonstrated, furnishes all the proof that can be needed of the xistence, even in the highest animals, of a 'propulsive power' resident in the essels; which, though usually subordinate to the Heart's action, is sufficiently trong to maintain the circulation by itself, when the power of the central organ s diminished. In this, as in many other cases, we may observe a remarkable apability in the living system of adapting itself to exigencies. In the acardiac Fœtus, the muscles of the vessels supply the place of the heart, up to the period of birth; after which, of course, the circulation ceases, for want of due aëration of the blood.

250. *Emigration of White Corpuscles and Diapedesis of the Red.*—One of the most frequent results of the inflammatory process is the formation of Pus, a serous or albuminous fluid holding a large number of corpuscles in suspension, the origin of which has been the object of much recent investigation. The cells are spherical, about the size of the white corpuscles of the blood, with softly-shaded contours and numerous granules in their interior. They contain one, two, or more nuclei. By Virchow* they were considered to be derived essentially from the proliferation of epithelial cells, and of connective-tissue corpuscles, and there can be no doubt that all intermediate stages between healthy epithelial cells and connective-tissue corpuscles, and pus-corpuscles, may be traced in inflammation, but numerous observers have noticed that under certain altered physical conditions of the circulation, an escape, both of the white and of the red corpuscles, takes place from the interior of the vessels into the adjoining tissues. This phenomenon was first observed in 1843, by Dr. W. Addison,† and was noticed to occur in inflammation by Waller,‡ who in a remarkable manner fully corroborated Addison's observation, declaring that he had seen the corpuscles protruding half-out of the vessels; whilst Addison had already arrived at the conclusion that pus-corpuscles of all kinds were only altered colourless blood-corpuscles. These statements, however, received little attention till the publication by Cohnheim§ of an essay on inflammation, in which he described the process of the passage both of the white and red corpuscles through the walls of the capillaries, and even of tolerably thick-walled veins, in detail.‖ The passage of the white corpuscles through the walls of the vessels appears to be due to some physical alteration in the walls of the vessel, reducing their tenacity, and permitting the colloidal substance of the corpuscles to penetrate them in a mode essentially similar, as Norris showed, to that by which a solid body may be made to traverse the thin film of a soap-bubble. This process is probably aided by the amœboid

* See his "Cellular Pathology," *passim.*

† "Exper. and Pract. Researches on Inflammation," 1843.

‡ "Philosoph. Magazine," Oct. and Nov. 1846; Lister, "Phil. Trans.," 1859.

§ Virchow's "Archiv," 1867.

‖ Cohnheim's observations immediately attracted great attention, and though they have been opposed by Feltz, Robin's "Journ. de l'Anatomie," 7me Année, 1870–71, pp. 33 and 505; Picot, idem., p. 465, and a few others, they have received the support of so many good observers, as of Stricker, idem., No. 6, 1867; Prussak, "Sitzungsber. d. Wien. Akad.," Band lxvi. p. 13; Caton, "Journal of Anatomy and Physiology," 1871, vol. v. p. 35; Norris, "Proceed. Roy. Society," 1871, No. 129; Bastian, "Transactions of Pathological Society," 1868, vol. xix. p. 461; and Heller, "Centralblatt f. d. Med. Wiss.," 1870, p. 310; that the main fact of the escape of the corpuscles from the vessels may be regarded as incontrovertible. In a recent essay, Cohnheim, "Neue Untersuchungen über Entzundung," Berlin, 1873, has given his latest views upon the point.

movements of the white corpuscles, and in part also by the increased pressure of the blood.* That neither the increased pressure of the blood, nor the mere dilatation of the vessels are sufficient *per se* to lead to the emigration of the corpuscles, seems to be demonstrated by the fact that if any slight injury, as a pinch of moderate severity, be inflicted on a transparent structure, as the tongue of a frog, the vessels in the vicinity may be seen immediately to enlarge (the arteries being first affected), permitting a more rapid current to flow through them. The veins then enlarge, and afterwards the capillaries. This condition is maintained for some minutes, when the arteries begin to contract, and with the capillaries return to their normal condition. The veins, however, do not follow this process of contraction, and hence the blood-current in them becomes slower. As soon as this stage is reached—viz., dilated veins with retarded circulation, a very abundant adhesion of colourless blood-corpuscles to the walls of those veins is seen to take place sooner or later; however, if the injury has not been too severe, the veins commence also to contract, in consequence of which the blood-current becomes quicker, and at the same time the number of adherent colourless corpuscles diminishes, until finally the normal condition is re-established. Now, notwithstanding there have been temporarily present the condition of dilated veins, slower blood-current, and marked adhesion of colourless blood-corpuscles to the wall of the veins, as well as increased pressure in the capillaries during the dilatation of the arteries, no coloured or colourless corpuscles will be seen to pass through the walls of the vessels; on the other hand, by proceedings adapted to produce physical changes in the relations of the walls of the vessels to the blood, an abundant emigration of the white corpuscles can be produced almost at will. Thus, Stricker and Prussak have both shown, that after the subcutaneous injection of a small quantity of a ten per-cent. solution of common salt, under the skin of frogs and rabbits, a condition of the vessels is produced in which the red corpuscles readily escape from the vessels; the same occurs when the main vein of a limb is tied; and these observers regard the diapedesis of the red corpuscles as the result of some "active condition" of the *capillary wall*, a view that Cohnheim also adopts, whilst Bastian attributes it to an "active condition," that is to say, to amœboid movements of the *red* blood corpuscles themselves. The emigration of the white corpuscles may also be readily witnessed in the mesentery of a frog inflamed by mere exposure to air; under such circumstances the white corpuscles accumulate, apply themselves to the sides of the vessels, where they either remain stationary or slowly oscillate. In a little while small colourless projections are seen on the outer surface of the vascular coat. These subsequently become pyriform, and ultimately detach themselves from the vessels, appearing as colourless contractile amœboid corpuscles, with one or several nuclei; the whole process being accomplished in from one to two hours.† That the presence of white corpuscles in large numbers in the tissues is not sufficient to constitute suppuration is shown well in the remarkable experiments of Tarchanoff‡ upon the effects of curare. On placing frogs under the influence of this poison, he found that the number of white corpuscles in the blood underwent great diminution, whilst the propor-

* It is possible, as Purves ("Centralblatt f. d. Med. Wiss.," 1874, p. 654), Arnold (Virchow's "Archiv," 1873, Band lviii. 203), Thomas ("Centralblatt," 1874, p. 364), and some writers maintain, that pores, which they believe are naturally present between the epithelial cells of which the walls of the smaller vessels are composed may enlarge, but this requires further confirmation.

† See Cornil and Ranvier, "Manuel d'Histologie Pathologique."

‡ Tarchanoff, "Archives de Physiologie," 1875, p. 33. See also Drozdoff, "Journal de la Méd. Milit.," 1872.

ion of the red increased.* The white corpuscles were found to be accumulated in the tissues and in the lymphatic vessels and sacs, which last were distended with lymph. These effects, which must be admitted to modify the statements of Goltz (see § 155), M. Tarchanoff attributes to augmentation of blood-pressure, owing to paralysis of the vaso-motor nerves, leading to dilatation and freer current of blood through the smaller arteries, and to repose of the muscles, and arrest of the contractions of the lymphatic hearts; yet, notwithstanding the exodus of the white corpuscles, no suppuration resulted, and on the animals recovering from the effects of the curare, the white corpuscles quickly disappeared from the tissues, whilst the lymph sacs returned to their normal condition.†

5. *Movement of the Blood in the Veins.*

251. The Venous system takes its origin in the small trunks that are formed by the re-union of the Capillaries; and it returns the blood from these to the Heart. The structure of the Veins is essentially the same as that of the Arteries; but the fibrous tissue of which their middle coat is made up bears more resemblance to the areolar tissue of the skin, than it does to the true elastic tissue, and presents the distinguishing feature of laminæ running longitudinally as well as transversely; and the muscular fibre-cells are usually much fewer in number, and are sometimes wanting altogether,‡ as in the veins of the uterine portion of the placenta; the veins of the cerebral substance and pia mater; the sinuses of the dura mater; Breschet's veins of the bones; the venous channels of the corpora cavernosa in the male and female; and probably the venous channels of the spleen, all of which are unprovided with muscular structure. Minute capillaries ramify in their outer coats. The *elasticity* of the Veins is shown by the jet of blood which at first spouts out in ordinary venesection, when, by means of the ligature, a distension has been occasioned in the tubes below it. Though the walls of the veins are thinner, they yet resist pressure better than the arteries. In an experiment of Wintringham§ the Aorta burst when the pressure rose to 158 lbs., whilst the Vena Cava only gave way when it reached 176 lbs. A slight *contractility* on the application of stimuli, and on irritation of the sympathetic nervous fibres, has been observed; but this is not so decided as in the arteries. The whole capacity of the venous system is considerably greater than that of the arterial; the former is usually estimated to contain from two to three times as much blood as the latter, in the ordinary condition of the circulation; and when we consider the great proportion which the veins in almost every part of the body bear to the arteries, we shall scarcely regard even the larger of these ratios as exaggerated. Of course the rapidity of the movement of the blood in the two systems will bear an inverse ratio to their respective capacities; thus if, in a given length, the veins contain three times as much

* The proportion of red to white in a cubic millimetre in a healthy frog was as 200,375 : 10,412; in a curarized frog it was 514,436 : 6,759 in the same quantity.

† Tarchanoff's experiments are, as he himself points out, in accord with previous observations of Paschutin, to the effect that curare causes an augmentation of lymph (Ludwig's "Arbeiten," 1872, p. 197), of Genersich, that muscular movements favour the flow of the lymph through the lymphatics, of Ranvier ("Comptes Rendus," 20th Dec. 1869), and Emminghaus (Ludwig's "Arbeiten," 1874), that section of the nerves of a limb increases the flow of lymph, and, lastly, of Hammarsten (Ludwig's "Arbeiten," 1872), that dogs from which much lymph has been withdrawn contain a larger amount of oxygen in their blood.

‡ Prof. Kölliker, "Manual of Human Histology," Syd. Soc., vol. ii. p. 307. See also Eberth, art. 'Blood-vessels,' in Stricker's "Hum. and Comp. Histology," vol. i. 1870, p. 275.

§ "Experimental Inquiry," &c., 1740.

blood as the arteries, the fluid will move with only one-third of the velocity. In the jugular vein its rapidity is about eight inches per second. Speaking generally, circumstances causing diminution of blood-pressure by dilatation of the arterioles, as division of the spinal cord, render the blood-current slower in the Veins.* Even at their origins in the capillary plexus, the Veins are larger than the Arteries which terminate in the same plexus; so that wherever the arterial and venous networks form distinct strata, they are readily distinguished from each other. The Veins are remarkable for the number of *valves* which they contain, formed of duplicatures of the endothelium, between the component laminæ of which connective-tissue fibres are interposed; and also for the dilatations behind these, which, when distended, give them a varicose appearance. The valves are single in the small veins, the free edge of the flap closing against the opposite wall of the vein; in the larger trunks they are double; and in a few instances they are composed of three flaps. The object of these valves is evidently to prevent the reflux of blood; and we shall presently see that they are of important use in assisting in the maintenance of the venous circulation. They are most numerous in those veins liable to be compressed by surrounding muscles, and they are not found in the veins of the lungs, of the abdominal viscera, or of the brain, or in veins measuring less than one-eighth of an inch in diameter. In the veins near the heart, like the innominate, jugular, and subclavian veins, a very well-marked *venous pulse* may be observed, due to the regurgitation of the blood into these vessels during the systole of the heart. The venous pulse wave is propagated from below upwards, and with a speed which is proportionate to the tension of the vascular walls. The curves of the tracing are, of course, greatly exaggerated in cases of insufficiency of the tricuspid valves.

Fig. 160.

Tracing of the pulse of the jugular vein in a healthy adult.—*a*, *b*, contraction of right auricle; *b*, *c*, contraction of right ventricle; *c*, closure of aortic valve; *d*, closure of valves of pulmonary artery; *e*, *f*, diastole of the right ventricle.

252. The *pressure of the blood* in the veins varies not only in different veins but in the same vein at different periods. In the veins near the heart a negative pressure is shown when a manometer is introduced into them, amounting to 0·1 mm. of mercury in the case of the vena innominata, the right subclavian, and left jugular vein. This indicates that a suction power is exerted on the blood, which is essentially attributable to the respiratory movements of the chest, though in part also due to the dilatation of the heart; and is of importance, since it permits the entrance of the fluid contained in the lymphatic duct into the general circulation, which would otherwise, considering the low pressure under which the lymph moves, be impossible. In the veins more remote from the heart, the pressure, instead of being negative, becomes positive, amounting to 3 mm. of mercury in the external facial vein; 4·1 mm. in the brachial; 5·2 mm. in the internal facial; 9 mm. in a branch of the brachial; and 11·4 mm. (or about half an inch) in the crural vein.† The influence of the respiratory movements on the pressure of the blood in the veins is evident from the occurrence of the respiratory pulse long ago described by Haller, which may be seen in the veins of the neck and shoulder in thin persons and in those especially who are suffering from pulmonary disease. During inspiration the veins are seen to be partially emptied, owing to the descent of their contents into the chest in order to supply the vacuum

* In regard to this point see Cyon and Steinmann, "Bulletin de l'Acad. des Sciences de St. Pétersbourg," t. xvi. 1871, p. 266.

† See Jacobson and Recklinghausen, Virchow's "Archiv," Band xxxvi. p. 1.

which is created at the moment of the contraction of the diaphragm; whilst during expiration the veins become turgid in consequence of the check in front and the accumulation from behind. The complete collapse of the larger veins during inspiration is prevented, as Berard has pointed out, by adhesions of their walls to surrounding parts.* The pressure of the blood in the veins will be augmented by a general increase in the quantity of blood in the system, and by increase in the force and frequency of the heart's beats, except that such increase would, in the first instance, occasion more rapid and complete depletion of the venous system. The blood-pressure in the pulmonary artery has been investigated by several observers, and has been found to be 3 times less than that in the carotid in the dog, 4 times less in the rabbit, and 5 times less in the cat. Other estimates are that the pressure in the pulmonary artery is to that of the aorta as 1 : 3; as 1 : 2·5; and 1 : 1·85. Hering, in a case of ectopia cordis in a calf, introduced glass tubes of equal diameter through the walls of the two ventricles, and found that the blood rose 21 inches in that in the right ventricle, and 33·4 inches in that in the left ventricle, which is in the proportion of 1 : 1·6. An agency which certainly assists the venous circulation in some animals is the rhythmical contraction of the walls of the Veins which has been observed to occur 8 to 10 times per minute in the transparent membrane of the wing of the Bat, the amount of contraction being about one-fourth of the diameter of the vessel (Wharton Jones). The same phenomenon repeated 5 or 6 times per minute has been observed by Schiff† and Vulpian‡ in the veins of the ear, and by Wagner§ in the vessels of the iris of the rabbit. It has also been shown by Mr. Wharton Jones|| that the lymphatic hearts of the eel and frog are to be regarded as exerting an auxiliary agency on the general circulation, propelling their contents at certain intervals into the veins. The walls of these hearts are composed of unstriped rhythmically contractile muscular fibrils which contract under the influence of the spinal cord.¶

253. One of the most powerful of the general causes which influence the Venous circulation is doubtless the frequently-recurring *pressure of the muscles* upon their trunks. When quiescent the circulation in muscles is extremely slow, but whenever contraction takes place, a portion of the Veins of the part will undergo compression; and as the blood is prevented, by the valves in the Veins, from being driven back into the small vessels, it is necessarily forced on towards the heart.** As each set of muscles is relaxed, the veins compressed by it fill out again, to be again compressed by the renewal of the force. That the general Muscular movement is an important agent in maintaining the circulation at a point above that at which it would be kept by the action of the heart and arterial system alone, appears from several considerations. The pulsations are diminished in frequency by rest, accelerated by exertion, and very much quickened by violent effort. In all kinds of exercise, and in almost every sort of effort, there is that alternate contraction and relaxation of particular groups of muscles, which has been just mentioned as affecting the flow of blood through the veins; and there can

* Berard, "Cours de Physiologie," t. iv. p. 62.
† "Archiv f. Physiol. Heilk.," 1854, t. xiii. p. 521.
‡ "Comptes Rendus de la Société de Biologie," 1856, p. 183.
§ "Archiv f. Ophthalmol.," Band xii. Heft ii. p. 1.
|| "Proceed. of the Roy. Soc.," 1868, Nos. 98, 101, and 102.
¶ See Eckhard, "Beiträge," No. vii. p. 167.
** Sadler, 'Ueber den Blutstrom in den ruhenden, verkürzten und ermüdeten Muskeln des lebendes Thieres,' in Ludwig's "Arbeiten," 1870, p. 77. Also Sczelkow, in "Wiener Sitzungsberichte," Band xlv.

be little doubt that the increased rapidity of the return of blood through them is of itself sufficient cause for the accelerated movements of the heart. When a large number of muscles are put in action after repose, as is the case when we rise up from a recumbent or a sitting posture, the blood is driven to the heart with a very strong impetus; and if that organ should be diseased, it may arrive there in a quantity larger than can be disposed of; so that sudden death may be the result. Hence the necessity for the avoidance of all sudden and violent movements on the part of those who labour under either functional disorder or structural disease of the centre of the circulation.

254. The Venous circulation is much more liable than the Arterial to be influenced by the force of gravity; and this influence is particularly noticeable when the tonicity of the vessels is deficient.—The following experiments, performed by Dr. C. J. B. Williams,* to elucidate the influence of deficient firmness in the walls of the vessels, and of gravitation, over the movement of fluids through tubes, throw great light on the causes of *venous congestion*:—A tube with two equal arms having been fitted to a syringe, a brass tube two feet long, having several right angles in its course, was adapted to one of them, whilst to the other was tied a portion of a rabbit's intestine four feet long, and of calibre double that of the brass tube, this being arranged in curves and coils, but without angles or crossings. When the two tubes were raised to the same height, the small metal tube discharged from two to five times the quantity of water discharged in a given time by the larger but membranous tube; the difference being greatest when the strokes of the piston were most forcible and sudden, by which the intestine was much dilated at its syringe-end, but conveyed very little more water. When the discharging ends were raised a few inches higher, the difference increased considerably, the amount of fluid discharged by the gut being much diminished; and when the ends were raised to the height of eight or ten inches, the gut ceased to discharge, each stroke only moving the column of water in it, and this subsiding again, without rising high enough to overflow.—When the force of the stroke increased, the part of the intestine nearest the syringe burst. From these experiments it is easy to understand how any deficiency of "tone" in the Venous system will tend to prevent the ascent of the blood from the depending parts of the body, and will consequently occasion an increased pressure on the walls of the vessels, and an augmentation in the quantity of blood they contain. All these conditions are peculiarly favourable to the escape of the watery part of the blood from the small vessels; and this may either infiltrate into the areolar tissue, or it may be poured into some neighbouring serous cavity, producing dropsy. Thus it happens that such effusions may often be traced to that state of deficient vigour of the system which peculiarly manifests itself in want of tone of the blood-vessels; and that it is relieved by remedies which restore this. In many young females of leuco-phlegmatic temperament, for example, there is a tendency to swelling of the feet, by œdematous effusion into the areolar tissue, in consequence of the depending position of the limbs; the œdema disappears during the night, but returns during the day, and is at its maximum in the evening. And the congestion which frequently manifests itself in the posterior parts of the body, towards the close of exhausting diseases in which the patient has lain much upon his back, is attributable to a similar cause; of such congestion, effusions into the various serous cavities are frequent results; and such effusions, taking place during the last hours of life, are often erroneously regarded as the source of death. To the same cause we are to attribute the varicose state of the veins of the leg, which is so common amongst

* "Principles of Medicine," 2nd edit., p. 188.

persons of relaxed fibre, and especially in those whose habits require them to be much in the erect posture; and this distension occasionally proceeds to complete rupture, the causes of which are fully elucidated by the experiments just cited. A peculiar humming sound may be heard in the veins of the neck when a stethoscope is placed and slight pressure exercised just above the clavicle, especially on the right side.* This may either be continuous or be rhythmical and synchronous with the diastole of the heart or with the act of inspiration. It is caused by the vibration of the walls of the vessels, caused by the eddy of the blood flowing from the narrower portion of the jugular above into the larger channel presented by its dilatation below; as a pathological symptom it is particularly perceptible in those in whom the walls of the veins are flaccid, as in anæmic patients.

255. Attempts have been made to ascertain the mode in which the blood is distributed through the body, the methods employed having been either by freezing the subject and determining the quantity of blood in each part, or by rapidly removing the several organs during life, and collecting the blood which flows from them and that which they still retain. Neither method gives more than approximative results; but, proceeding in this way, Ranke estimated that in the living and quiescent rabbit the blood was nearly equally divided between the muscles, the liver, the heart and arteries, and the whole of the remaining organs. The quantity in each part of the body is, however, undergoing constant alteration, the variation being essentially dependent upon its functional activity. The difference has been observed to amount to as much as 30 or even 47 per cent. Well-marked examples of great differences in the quantity of blood present may be observed in quiescent and active glands, in the full and empty stomach, and a principle of compensation may be noticed to occur in many organs—the mind, for example, being less active during digestion; the kidneys secreting less when the vessels of the skin are dilated and free transpiration is taking place. The variations in the quantity of blood in an extremity may be demonstrated by an instrument named a Plethysmograph, constructed by Mosso, and which consists essentially of a glass cylinder, into which the arm or leg can be introduced, and by means of a caoutchouc band be made to fit water-tight to it. The space between the limb and the tube is filled with water, the pressure of which can be increased or diminished by raising or lowering a vessel filled with water; in connection with the cylinder is also a manometer, to which is attached a registering apparatus. The variations of volume exhibited by the extremity in the cylinder are found to be referable to the arterial pulsations, the curves of which resemble those of the pulse; secondly, to respiratory movements, strong inspiration augmenting the venous current and enfeebling the arterial flow, and *vice versâ;* active respiration and arrest of respiration alike cause diminution of volume, whilst it is increased by straining and coughing; thirdly, to variations in the activity of the vaso-motor ganglia, causing periodic variations of volume by modifying the size of the smaller arteries; fourthly, to differences in the position of the limb, causing variation of hydrostatic pressure; fifthly, to muscular activity or quiescence, the former facilitating the flow of blood through the veins; sixthly, to mental activity, which, by withdrawing blood to the large intracranial plexus of vessels, diminishes the volume of the extremities; lastly, to compression of the arteries or veins.

* Landois, "Lehrbuch der Physiologie, 1879, p. 191.

6. *Peculiarities of the Circulation in different Parts.*

256. In several portions of the Human body there are certain varieties in the distribution and in the functional actions of the blood-vessels which should not be omitted in a general account of the Circulation.—Of these, we have in the first place to notice the apparatus for the *Pulmonary* circulation; the chief peculiarity of which is, that *venous* blood is sent *from* the heart, through a tube which is arterial in its structure, whilst *arterial* blood is returned *to* the heart, through a vessel whose entire character is that of a vein. The movement of the blood through these is considerably affected by the physical state of the lungs themselves; being retarded by any causes which can occasion pressure on the vessels (such as over-distension of the cells with air,* obstruction of their cavity by solid or fluid depositions, or by foreign substances injected into them, &c.); and proceeding with the greatest energy and regularity when the respiratory movements are freely performed.—The *Portal* circulation, again, is peculiar, in being a kind of offset from the general or systemic circulation, and also in being destitute of valves; and it may be surmised, with much probability, that the purpose of their absence is to allow of an unusually free passage of blood from one part of that system to another, during the very varying conditions to which it is subjected. The Vena Portæ resembles other veins in being formed by the union of smaller veins, and it receives the venous blood which has traversed the capillaries of the stomach, intestines, and spleen; but, instead of opening directly into the Vena Cava, it is peculiar in breaking up, when it arrives at the liver, into a second system of capillaries, which are distributed throughout that organ; and it is only after the hepatic capillaries have reunited to form the Hepatic vein that the blood is transmitted to the heart through the Vena Cava. The presence of the second set of capillaries renders the circulation slower in the portal system of vessels than in any other part of the body.—The *Renal* circulation, again, presents certain peculiarities that resemble those of the portal circulation. In this case the arteries divide and subdivide, till at length a small afferent branch enters the dilated extremity of a urinary tubule and here forms a *glomerulus*, or convoluted mass of capillaries, which may be compared to the capillary plexus on the walls of the intestines. From the glomerulus issues an efferent artery, comparable to the Vena Portæ, which again breaks up into a capillary plexus surrounding the urinary tubules, just as the Vena Portæ divides into capillaries, permeating the liver. Finally, the renal capillary plexus discharges its contents into veins which, becoming successively larger, form the renal vein.—Another very important modification of the Circulating system is that which presents itself within the *Cranium*. From the circumstance of the cranium being a closed cavity, which must be always filled with the same total amount of contents, the flow of blood through its vessels is attended with some peculiarities. The pressure of the atmosphere is here exerted, rather to keep the blood in the head than to force it out; and it might accordingly be inferred that, whilst the quantity of cerebral matter remains the same, the amount of blood in the cranial vessels must also be invariable. This inference appeared to derive support from the experiments of Dr. Kellie,† who found, on bleeding animals to death, that, whilst the remainder of the body was completely exsanguine, the usual quantity of blood remained in the arteries and veins of the cranium; but that, if an opening was made in the skull, these vessels were then as completely emptied as the rest.

* See Quincke and Pfeiffer, 'Ueber den Blutstrom in die Lungen,' Reichert und Du Bois-Reymond's "Archiv," 1871, p. 90.

† "Edinburgh Medico-Chirurgical Transactions," vol. i.

In the experiments performed by Küssmaul and Tenner,* it was found on trephining the skull and compressing the carotids, that the brain, especially after removal of the dura mater, became very pale, and retreated from the opening to so great an extent as to form a cup 2½ mm. in depth; whilst, on releasing the pressure, it assumed a deep rose colour and became convex. When, however, they luted a piece of glass air-tight into the hole made by the trephine, as suggested by Donders, the phenomena were no longer the same, for no movement of any kind could then be perceived in the brain, which remained in all cases immovably in contact with the glass plate; but the same changes in the tint of the cerebral substance, on checking and again restoring the current in the arteries, were observed. Observations of a similar nature were made by Mr. Durham† and Dr. Hammond,‡ by whom it was noticed that the condition of the brain varied to a remarkable degree in the sleeping and in the waking states, being paler and anæmic in the former, and comparatively congested in the latter. These experiments, therefore, appear to furnish indisputable evidence that the circulation of blood through the Brain varies with the general conditions of the vascular system, and is not, as Dr. Kellie's experiments appeared to show, independent of them. In M. Jolly's experiments a manometer luted into the skull of dogs showed a positive pressure, which, rising with expiration and falling with inspiration, was sufficient in general to support a column of water varying from one to six inches in height. In rabbits it was about half this amount, and occasionally became negative. The pulse in dogs caused a variation of from 5 to 10 mm. Compression of the carotids produced but little effect, but the pressure slowly rose when the jugular veins were compressed.§ Moreover, in disordered states of the circulation the quantity of blood in the vessels of the cranium may be for a time diminished by a sudden extravasation, either of blood or serum, into the cerebral substance; and the amount of interior *pressure* upon the walls of the vessels may also be considerably altered, even when there is no difference in the *quantity* of fluid contained in them.‖ It seems highly probable that in the delicate and extensive system of capillaries found in the pia mater and choroid plexus, a provision is made by which a large quantity of cerebro-spinal fluid can be effused or absorbed in a short space of time, to compensate for sudden changes in the balance of the circulation.

257. The *Erectile Tissues* present another curious modification of the ordinary vascular apparatus. The chief of these are the corpora cavernosa in the penis of the male, and in the clitoris of the female; the collection of similar tissues round the vagina and in the nymphæ and uterus (Rouget) of the female; and the nipple in both sexes. In all these situations, erection may be produced, and in the case of the penis, *emissio seminis* may be effected,

* See their Essay (Syd. Soc. Translation), p. 39, et seq., 1859.

† "Guy's Hosp. Rep.," 1860, p. 149.

‡ "New York Med. Journ.," 1865, quoted in the 'Physiology of Man,' by Dr. Austin Flint.

§ See F. Jolly, "Untersuchungen über den Gehirndrück und über die Blutbewegung im Schädel," Wurzburg, 1871; G. Althaun, "Beiträge zur Physiologie und Pathologie der Circulation," 1871. Pagenstecher, "Experimente und Studien über Gehirndrück;" and Cappie, "The Relation of the Cranial Contents to the Pressure of the Atmosphere," 1874; R. Vance, 'The Encephalic Circulation,' "New York Med. Record," 1877, p. 291.

‖ The results of the experiments of Dr. G. Burrows ("Medical Gazette," April and May, 1843) fully confirm the views stated above. Pagenstecher has shown that from 2·9 to 6·5 per cent. of the cubic capacity of an animal's skull may be occupied by injection of wax and tallow through a trephine aperture before symptoms of pressure supervene. In other words, that taking the capacity of the skull to be 1300–1400 cub. cm., from 37·7–40·6 cub. cm. as a mean, or 84·5–90·0 cub. cm. as maximum of blood may be effused without evidence of pressure.

by local irritation. The erectile tissue appears essentially to consist of a plexus of veins with varicose enlargements, enclosed in a fibro-muscular envelope with trabecular partitions.* In the penis, as first pointed out by Prof. Müller,† there are two sets of arteries; those of one set, destined for the nutrition of the tissues, communicating with the veins in the usual way, through a capillary network; whilst the others, termed by him the "helicine arteries," are short, tendril-like branches which project into the veins (covered, however, by their endothelium), sometimes singly, and sometimes in tufts, ending abruptly by dilated extremities. These arteries are accompanied by a special system of longitudinal bundles of muscles, the fibres of which become inserted into the middle coat at various points (Stilling, Stein). The dilated ends of the helicine arteries usually communicate directly with the venous cavities, since injection thrown into the former generally fills the latter, and Kölliker states that he has frequently found them giving-off delicate, almost capillary vessels, which discharge themselves into the venous spaces. The nerves implicated in producing erection in the dog were found by Eckhard‡ to be, first, the *Nn. pudend. communes* proceeding from the sciatic plexus, and supplying the musculi ischio-cavernosi, the corpora cavernosa of the penis, and membranous portion of the urethra; and, second, the *Nervi erigentes* proceeding from the sacral nerves and entering the hypogastric plexus. This plexus contains minute ganglia, communicates with the posterior mesenteric plexus, and furnishes branches to the bladder, prostate gland, rectum, and membranous portions of the urethra. After division of the former, or common pudendal nerves in the dog, Eckhard found it impossible to produce erection of the penis or emission of semen by direct irritation of the penis. The Nervi erigentes are, undoubtedly, the chief excitors to erection, for on exposing and irritating them, swelling of the penis, gradually proceeding forwards to the glans, immediately commenced. Erection may also occur as a result of certain emotional conditions of the mind, the influence of which is probably transmitted through the Sympathetic nerve, as it may be experienced even in cases of paraplegia; whilst, according to Legros,§ after section of the sympathetic fibres distributed to an erectile organ no erection occurs. The precise mode in which the nerves act is still unknown,‖ but there are grounds for believing that both the male and female organs are preserved in a quiescent state by a tonic influence exerted over the vessels by centres situated in the lower part of the spinal cord. In the venereal orgasm, however, inhibitory centres are excited, which restrain the action of the spinal cord and lead to dilatation of the vessels and increased flow of blood through the organ; Eckhard, indeed, relates that in his experiments he obtained eight times more blood from the veins of the penis in a given time at the period of erection than during the intervals. The ischio-cavernosi and bulbo-cavernosus muscles probably afford

* See A. W. Stein, "New York Med. Journal," June, 1872, for an account of the Histology and Physiology of the Penis.

† 'Entdeckung der bei der Erection wirksamen Arterien,' in Müller's "Archiv," 1835, p. 202. The views of Müller, though opposed by Valentin (Müller's "Archiv," 1838, p. 182), Weber, Arnold, Béclard, and others, as well as recently by Rouget, "Journal de l'Anatomie," t. i. p. 326, and Langer, "Wien. Sitz.," xlvi. 1863, p. 120, who consider the helicine arteries to be for the most part, if not altogether, artificial products consequent on the difficulty of forcing injection into the tortuous vessels of the trabeculæ, have been supported by the great authority of Henle ("Handbuch d. Mensch. Anatom.," 1866, p. 402). See also Robin, pamphlet "On the Erectile Tissues;" Vulpian, "Leçons sur l'Appareil Vasomoteur," 1875, p. 161; Krause, "Histologie," 1876, p. 273; Toldt, "Lehrbuch der Gewebelehre," 1877, p. 484.

‡ "Beiträge zur Anat. und Phys.," Giessen, 1863 and 1867, p. 71.

§ "Gaz. Méd. de Paris," 1866, No. 6.

‖ For different views see Kölliker, loc. cit.; Rouget, "Archives de Physiologie," 1868, p. 671; Goltz, Pflüger's "Archiv," Band vii. 1873, p. 346; Vulpian, "Leçons sur l'Appareil Vasomoteur," 1875, p. 161, et seq.

some assistance in completing and strengthening the act of erection by compressing the veins which return the blood from the penis, but they are clearly unable to effect it by their own act, and it is obvious that no analogous power can be exerted in other erectile organs, as the nipple. Their centres, according to Goltz,* are situated in the lumbar region of the spinal cord, and here also is in all probability an inhibitory centre governing their action as well as that of the *sphincter ani.*

CHAPTER IX.

OF RESPIRATION.

1. *Nature of the Function: and Provisions for its Performance.*

258. The Nutritive fluid, in its circulation through the capillaries of the system, undergoes great alterations, both in its physical constitution and in its vital properties. It gives-up to the tissues with which it is brought into contact some of its most important elements; and at the same time it is made the vehicle of the removal, from these tissues, of ingredients which are no longer in the state of combination that fits them for their offices in the Animal Economy. To separate these ingredients from the general current of the circulation, and to carry them out of the system, is the great object of the Excretory organs; the importance of whose respective functions will vary, it is very evident, with the amount of the ingredient which they have to separate, and with the deleterious influence which its retention would exert on the welfare of the system at large. Of all these injurious ingredients, Carbonic Acid is without doubt the one most abundantly introduced into the nutritive fluid; and it is also most deleterious in its effects on the system, if allowed to accumulate.—We find, accordingly, that the provision for the removal of this substance from the blood is one of peculiar extent and importance, especially in the higher forms of animals; and further, that instead of being affected by an operation peculiarly *vital* (like other acts of Excretion), its performance is secured by being made to depend upon simple *physical* conditions, and is thus comparatively little susceptible of derangement from disorder of other processes. All that is requisite for it is the exposure of the Blood to the influence of the atmospheric air (or, in aquatic animals, of air dissolved in water),† through the medium of a membrane that shall permit the "diffusion of gases;" an interchange then taking place between the gaseous matters on the two sides—Carbonic acid being exhaled from the Blood, and being replaced by Oxygen from the air. Thus, the extrication of Carbonic acid is effected in a manner that renders it subservient to the introduction of that element which is required for all the most active manifestations of vital power; and it is in these two processes conjointly, not in either alone, that the function of Respiration essentially consists.—We shall now inquire into the sources from which Carbonic acid is produced in the living body, and the causes of the demand for Oxygen.

259. The vital activity of the organism at large involves a continual change in its constituent parts; and those which (so to speak) live the fastest, usually

* Goltz, Pflüger's "Archiv," Band vii. 1873, p. 582.

† Whilst air contains about one-fifth of its volume of oxygen gas, water contains only one-two hundred and fiftieth of its volume. The feebleness of the respiratory processes which this implies in aquatic animals is in part compensated for by the ready solubility of carbonic acid gas in water, which facilitates its escape from the system, and the circumstance that the espiratory organs are actually floating in the oxygenated medium.

die the soonest, and pass most readily into decay (CHAP. X. SECT. 1). Hence in the very performance of the Organic functions which concur to effect the Nutrition of the body, there is a constant source of disintegration; and one of the chief products of the decay of the tissues, which is consequent upon their loss of vitality, is Carbonic acid.—The exchange of the Oxygen contained in the blood for the Carbonic acid generated in the tissues constitutes the process of "internal respiration," and takes place in all parts of the body. On the other hand, the exchange of the Oxygen contained in the air for the Carbonic acid constantly accumulating in the blood which takes place in the lungs and skin, constitutes the process of "external respiration." Thus, the *most general* object of the Respiratory process, which is common to all forms of organised being, is the extrication of this product from the system; and the demand for aëration hence arising, will vary with the activity of the nutritive operations. Now the rate of life, and consequently the amount of disintegration, in any organized structure, depend in great measure upon the temperature at which it is maintained; and thus it happens that the production of Carbonic acid from this source, at the ordinary rate of vital activity, is much more rapid in "warm-blooded" than in "cold-blooded" animals, and that the former suffer far more speedily than the latter from the privation of air. But when the temperature of the Reptile is raised by external heat to the level of that of the Mammal, its need for respiration increases, owing to the augmented waste of its tissues. When, on the other hand, the warm-blooded Mammal is reduced, in the state of hybernation, to the level of the cold-blooded Reptile, the waste of its tissues diminishes to such an extent as to require but a very small exertion of the respiratory process to get rid of the Carbonic acid, which is one of its chief products. And in those animals which are capable of retaining their vitality when they are frozen, or when their tissues are completely dried up, vital activity and disintegration are alike entirely suspended, and consequently there is no Carbonic acid to be set-free.

260. But another source of Carbonic acid to be set-free by the Respiratory process, and one which is peculiar to animals, consists in the rapid changes which take place in the Muscular and Nervous tissues, in the very act of performing their peculiar functions; the development of the Muscular and of the Nervous forces involving, as the very condition of their production, a change in the substance of these tissues respectively; in which change a large quantity of oxygen is consumed, and a large amount of carbonic acid is generated. Hence in Man, as in all Animals, in which the Nervo-Muscular apparatus constitutes the essential part of the organism, a powerful demand for Respiration is created by its activity; the amount of oxygen taken-in, and of carbonic acid exhaled, being determined, *cæteris paribus*, by the degree in which this apparatus is exercised.—That Carbonic acid is set-free ready-formed by the muscles, and is not exclusively generated by the oxidation of the products of their disintegration after the reception of these into the blood-current, has been shown by the experiments of Dr. G. Liebig,* who found that carefully-prepared frogs' muscles absorb oxygen and exhale carbonic acid so long as their contractility lasts, even when they have been completely deprived of blood. In the similar experiments more recently made by M. Paul Bert† it clearly appears that whilst the muscular tissue on account of its large mass plays the most important part in those internal processes which he has

* "Bericht d. Akad. d. Wissensch. zu Berlin," 1850, §§ 339–347.

† P. Bert, "Leçons sur la Physiologie comparée de la Respiration," Paris, 1870, p. 30, et seq. In these experiments M. Bert found that:—

termed the "respiration of the tissues," yet that analogous changes occur in every tissue and organ in the body.* It must not, however, be too hastily assumed that the phenomena here witnessed are those of simple oxidation, since the absorption of Oxygen and the extrication of Carbonic acid are probably only the first and last links in a long series of decompositions.

261. Besides these sources of Carbonic acid which are common to all Animals, there is another which is restricted (or nearly so) to the two highest classes, Birds and Mammals; these being distinguished by their power of maintaining a constantly-elevated temperature. A part of this heat is generated by the oxygenation of the components of their disintegrating tissues, and of their blood, the metamorphosis of which takes place at a very rapid rate; but where this is not sufficient, their power of maintaining their temperature depends upon the *direct* combination of certain elements of the food with the oxygen of the air, by the combustive process.—The quantity of Carbonic acid that is generated directly from the elements of the food seems to vary considerably in different animals, and in different states of the same individual. In the Carnivorous tribes, which spend the greater part of their time in a state of activity, it is probable that the quantity which is generated by the waste or metamorphosis of the tissues is sufficient for the maintenance of the required temperature; and that comparatively little of the carbonic acid set-free in respiration is derived from the direct combustion of the materials of the food. But in Herbivorous animals of comparatively inert habits, the amount of metamorphosis of the tissues is insufficient; and some part of the food, consisting as it does of substances that undergo combustion with great facility, probably enters into direct combination with the oxygen of the air, and thus compensates for the deficiency.† In Man and other animals, which can sustain considerable variations of climate, and can adapt themselves to a great diversity of habits, the quantity of carbonic acid formed by the direct combination of the elements of the food with the oxygen of the air, will differ under different circumstances. It will serve as the *complement* of that which is formed in other ways; so that it will diminish with the increase, and will increase with the diminution of muscular activity. It will also vary in an inverse ratio to the external temperature, increasing with its diminution (as more heat must then be generated), and diminishing with its increase; the effect of external heat being thus precisely opposite, in the warm-blooded animal, to that which it exerts on the cold-blooded.—In all cases, if a

Grammes.		Cub. cent. of Oxygen.	Cub. cent. of Carbonic Acid.
100 of muscle	Absorbed	50·8	Exhaled 56·8
„ of brain		45·8	42·8
„ of kidney		37·0	15·6
„ of spleen		27·3	15·4
„ of testis		18·3	27·5
„ of bone and marrow crushed		17·2	8·1

It is worthy of notice that M. Bert finds in corroboration of Spallanzani's experiments that the larger the proportion of oxygen present in the air to which the tissues are exposed, the more freely it is absorbed; the proportion of carbonic acid gas exhaled, however, is not correspondingly increased.

* The statement of MM. Estor and St. Pierre, that the formation of carbonic acid is most energetic in the arterial system (Robin's "Journal de l'Anatomie," 1865, p. 302), has been refuted by Hirschmann (Du Bois-Reymond's "Archiv," 1866, p. 502), and Hoppe-Seyler ("Med. Chem. Untersuch.," Berlin, 1867, p. 295).

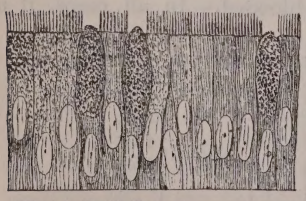
† Thus Ludwig and Scheremetjewsky found that if an easily combustible substance like glycerin or lactate of soda be injected directly into the blood, the absorption of O and elimination of CO_2 were immediately and considerably increased (Ludwig's "Arbeiten," 1868).

sufficient supply of food be not furnished, the store of fat is drawn upon; and if this be exhausted, the animal dies of cold. To recapitulate, then, the sources of demand for Oxygen and production of Carbonic acid in the animal body are threefold.—I. The continual decay of the tissues common to all organized bodies, which is favoured by whatever promotes their vital activity, and is retarded by every influence that depresses it.—II. The metamorphosis peculiar to the Nervous and Muscular tissues, which is the very condition of the production of their power, and which, therefore, bears a direct relation to the degree in which they are exerted.—III. The direct oxidation of some of the constituents of the food which varies the proportion in accordance with the amount of heat to be generated.

262. The activity of the process of respiration in any animal is, as a general rule, in direct proportion to the smallness of the corpuscles of its blood; for these, as has already been shown (§ 176), are the carriers of oxygen; and it is evident that a given weight of smaller globules will offer a larger surface for the absorption of oxygen than an equal weight of larger corpuscles. Hence in Fishes and Reptiles, which possess larger corpuscles, the provision for the aëration of the blood is much less perfect, and the amount of oxygen absorbed, and of carbonic acid eliminated, is considerably smaller than in the case of Mammals and Birds, the corpuscles of whose blood are remarkably minute. At the same time, the size of the lungs in the latter classes is far less in proportion to their bulk than in most Reptiles; but this diminution is more than compensated by the minute subdivision of their cavities, by the peculiarity of the distribution of their blood-vessels, and by the arrangements whereby a continual and rapid interchange, both of the blood and of the air, is provided for.—The following are the points of most importance in the structure of the Human Lung:*—The walls of the larger *bronchi* are composed independently of the tunica adventitia of four structurally distinct layers. Of these the outermost (*a*, Fig. 162) is a fibrous layer of dense connective-tissue in which cartilaginous laminæ, conferring firmness and elasticity on the tubes, are imbedded. The next (*b*) is a muscular layer composed of compact circularly-arranged fasciculi of smooth muscular tissue. The third is the internal fibrous layer (*c*), composed of tolerably regularly-arranged longitudinal bundles of thick elastic fibres, which on section give a sinuous outline to the interior of the tube. The innermost part of this layer is condensed into a hyaline layer, and upon this last or so-called basement membrane rests the ciliated columnar epithelium that forms the fourth layer (*d*). Intervening here and there amongst the ciliated columnar cells are E. Schulze's *cup*, *goblet*, or *chalice cells* (*b*, Fig. 161). These are filled with the mucous mass through which numerous highly-refractile granules are distributed. Imbedded in the outer fibrous layer of the larger bronchi are numerous mucous glands, the ducts of which run inwards, are lined with columnar epithelium, and open by trumpet-shaped

Fig. 161.

a *b*

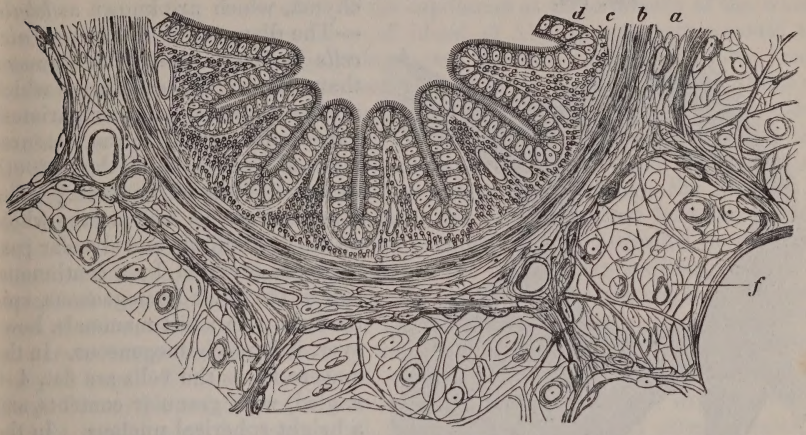


Ciliated Epithelium from a bronchial twig 1-6th of an inch in diameter.—*a*, ciliated columnar epithelial cells; *b*, goblet cells. From the Dog, magnified 320 diameters.

* For an account of the principal forms of Respiratory apparatus among the lower Animals, see "Princ. of Comp. Phys.," chap. vi.; also the Memoir by Mr. Rainey in the "Med.-Chirurg. Trans.," vol. xxviii; and Prof. Kölliker's "Manual of Human Microscopic Anatomy," 1860, Lond. For excellent general accounts of the structure of the Human Lung, see Waters's "Fothergillian Essay," London, 1860; Williams, in the Supplement of the "Cycl. Anat. and Physiology;" and F. E. Schulze in Stricker's "Manual of Histology" (Syd. Soc. Trans.), vol. ii. 1872, p. 63, on whose essay the following description is founded.

orifices. They cease with the cartilaginous plates between which only they ultimately appear. The smaller bronchi, or those having a diameter of about one-fiftieth of an inch, differ from the foregoing chiefly in the thinness of their

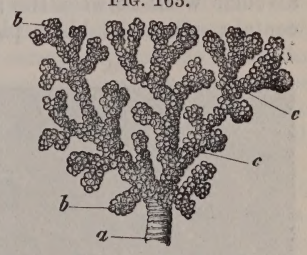
Fig. 162.



Part of a transverse section of a bronchial tube from the Pig, having a diameter of about 1-60th of an inch, magnified 240 diameters.—*a*, external fibrous layer; *b*, muscular layer; *c*, internal fibrous layer; *d*, epithelial layer; *f*, one of the surrounding alveoli.

external fibrous coat, and the absence in it of either cartilages or mucous glands, whilst the columnar ciliated epithelium becomes lower or more flattened, and finally at the termination of the bronchia in the alveolar passages the cells lose their cilia and the cup cells cease to appear. The bronchial tubes divide and subdivide, and at their termination (*a*, Fig. 163), open into canals known as the *alveolar passages*, the entrance of which is surrounded by a thick bundle of annular muscular fibre-cells forming a kind of sphincter.* The alveolar passages, *c*, *c*, are rather wider than the bronchia, from which they spring, and, after dividing dichotomously at acute angles from two to four times, terminate cœcally at a distance of from 1-12th to 1-6th of an inch from the extremity of each bronchial tube. In consequence of these ultimate processes gradually expanding towards their cæcal terminations they have been termed *infundibula*. Both the alveolar passages and the infundibula (air-sacs of Dr. Waters, which he describes rather differently from Schulze as forming a group of from 6 to 10 in number clustered around the extremity of every bronchial tube) are beset with numerous small polyhedric cavities with rounded angles and borders termed the *alveoli* or *air-cells* (Fig. 163); from ten to twenty of each may be counted on the interior of each infundibulum or air-sac. The length of the alveoli of ordinary size are about equal to their breadth; their total number has been estimated approximately at 1700 or 1800 millions, with a surface equivalent to 200 square metres (Küss).† The foundation layer of the alveolar wall is composed of a transparent structureless membrane, which in the thickest parts exhibits a distinctly fibrous character,

Fig. 163.



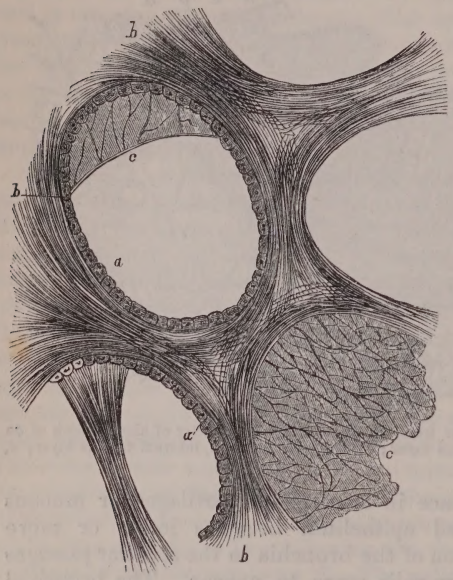
System of alveolar passages and infundibula from the margin of the Lung of a Monkey (Cercopithecus) injected with mercury, magnified 10 diameters.—*a*, terminal bronchial twig; *b*, *b*, infundibula; *c*, *c*, alveolar passages.

* Rindfleisch, "Centralblatt," 1872, p. 65.

† "Physiologie," 1873, p. 338.

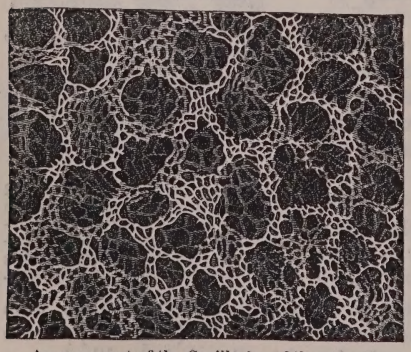
caused by the presence of numerous elastic* and muscular fibres.† The membrane is folded sharply at the margin of the air-vesicles (Fig. 164, *c*) so as to form a very definite border to them. The stronger septa divide off polyhedric portions of the alveolar parenchyma, which are known as *lobuli*. —The diameter of the human *air-cells* is about twenty times greater than that of the capillaries which are distributed upon their parietes; varying (according to the measurement of Weber) from the 1-200th to the 1-70th of an inch.‡ The inner surface as well as the whole of the infundibula and alveolar passages are invested by a continuous, and in the fœtus homogeneous, epithelium. In adult mammals, however, it is not homogeneous. In the mature fœtus the cells are flat, 4–6 angled, with granular contents, and a bright spherical nucleus. In the adult such cells are arranged in groups of two or four, separated by large, transparent, thin, structureless cells, which are either irregularly angular or sinuous in outline. These cover, though perhaps not quite continuously, the capillaries and all the folds and prominent edges. The granular spheroidal cells cover the alveolar walls between the meshes of the capillaries, and in adults constantly contain spheroidal black pigment granules. The capillary plexus (Fig. 165) is so disposed between the two layers which form the walls of two adjacent air-cells, as to expose one of its surfaces to each; by which provision the full influence of the air upon it is secured. The network of vessels is so close that the diameter of the meshes is scarcely so great as that of the capillaries which enclose them, and they often project into the cavity of the alveoli, either free or covered only by the flat cells above mentioned; indeed, it would be impossible to conceive of a method by which blood, whilst still retained within vessels, should be spread over a larger surface for aëration. And if not restricted

Fig. 164.



Air-cells of *Human Lung*, with intervening tissues.—*a*, epithelium; *b*, elastic trabeculæ; *c*, membranous wall, with fine elastic fibres.

Fig. 165.



Arrangement of the Capillaries of the air-cells of the *Human Lung*.

* Piso-Borme, Schmidt's "Jahrbuch.," 1868.

† Hirschmann and Chrzonsczczewsky, Virchow's "Archiv," 1866, p. 355.

‡ The dimensions given by Moleschott ("De Vesiculis Pulmonum Malpighianis") are very much less than these; the range of diameter being stated by him at between 1 120th and 1–1200th of an inch. The Author's own observations, however, lead him to regard Weber's and Kölliker's statements as very near the truth.

within vessels, it could not be ceaselessly and rapidly driven-on by the propulsive power of the heart, which acts no less efficiently upon the pulmonary circulation than upon the systemic, although the force exerted is much inferior, the resisting power being far less, in consequence of the shortness of the circuit. Estimating the surface of the capillaries at three-fourths of the whole surface of the alveoli, a thin layer of blood of 150 square metres would be exposed to the air, representing about two litres of blood; and it has been further calculated that it is renewed 10,000 times in the 24 hours (Küss).* Even making great allowance for error in these calculations, enough remains to show how extensive is the surface for the interchange of gases between the air and the blood.—Two systems of vessels, the pulmonary and the bronchial, transmit blood, though in very different proportions, through the lungs. In the former, which is by far the largest, the blood received from the system, deficient in oxygen and charged with carbonic acid, is propelled by the right ventricle through the pulmonary artery to the minute plexus of capillaries just described on the walls of the air-sacs and vesicles. From thence, having undergone aëration, it is returned to the left auricle of the heart, through the pulmonary veins, to be distributed by the left ventricle and arterial system to the body at large. The smaller system, which has been particularly examined by Prof. Turner,† consisting of the bronchial arteries and veins, with numerous minute branches of the intercostal, internal mammary, and other arteries, is distributed to the parts about the root of the lung, the large bronchial tubes, and the pulmonic pleura; some of its capillaries discharge themselves into the corresponding bronchial veins, whilst others terminate in the pulmonary system, and, there is reason to believe, play an important part in maintaining the circulation in cases where the pulmonary artery has been obliterated by disease. The *lymphatics* of the Lungs‡ arise either from branched cells in the alveolar septa, one of the branches opening between the epithelial cells into the cavity of the alveoli (pseudo-stomata of Klein); or, as Sikorski maintains, from the goblet cells of Schulze. In either case they form a plexus in the submucosa, and then run with, and partially or wholly invaginate branches of the pulmonary artery and vein. Cloetta found in the lung tissue inosit, uric acid, taurin, and leucin, besides the ordinary chemical constituents of the glandular textures, as albuminous compounds, collagen, chondrin, protagon, elastin, and mucin. In the fœtus, the tissue of the lungs contains a large number of cells rich in glycogen, which escape on pressure in the form of a milk-white fluid, but which are not found except under pathological conditions in the adult.

263. The contractility of the bronchial tubes (according to the experiments of Dr. C. J. B. Williams§) may be excited by electrical, chemical, or mechanical stimuli, applied to themselves. It is chiefly manifested in the smaller bronchial tubes, those of less than a line in diameter having been seen to contract gradually under the stimulus of galvanism, until their cavity was nearly obliterated; on the other hand, in the trachea and the larger bronchi, the cartilaginous rings prevent any decided diminution in the calibre of the tubes, and the muscular structure is much less distinct. It is doubtful whether the contractility can be immediately and visibly called into play by irritation of the Pneumogastrics,‖ but there is reason to think that the general tone of the

* Op. cit., 338.

† "Med.-Chir. Rev.," 1865, p. 209.

‡ See Wywodzoff, "Wien. Med. Jahrbücher," Band xi. p. 3. Sikorski, "Centralblatt, f. d. Med. Wiss.," 1870, p. 817. Klein, "Proceed. Roy. Soc.," Jan. 29, 1874.

§ "Report of the British Association for 1840," p. 411.

‖ Volkmann (Wagner's "Handwörterbuch," Band ii., Art. 'Nervenphysiologie,' p. 586), Longet ("Anat. et Physiol. du Système Nerveux," tom. ii. p. 289), and P. Bert ("Leçons sur la Physiologie comparée de la Respiration," Paris, 1870, p. 375) affirm that it can, whilst

muscular tissue in the lungs is dependent on this nerve. It is remarked by Dr. Williams, that the contractility of the bronchial muscles is soon exhausted by direct stimulation; but that it may in some degree be restored by rest, even when the lung is removed from the body. When the stimulation is long continued, however, as by intense irritation of the mucous membrane during life, the contractile tissue passes into a state which resembles the tonic contraction of muscular fibre. The contractility is greatly affected by the mode of death, and is remarkably diminished by the action of vegetable narcotics, particularly stramonium and belladonna; whilst it seems to be scarcely at all affected by hydrocyanic acid.—These facts are very important, as throwing light upon certain diseased conditions. It has long been suspected that the dyspnœa of Spasmodic Asthma depends upon a constricted state of the smaller bronchial tubes, excited through the nervous system, frequently by a stimulating cause at some distance; and there can be now little doubt that such is the case. The peculiar influence of stramonium and belladonna, in diminishing the contractility of these fibres, harmonizes remarkably with the well-known fact of the relief frequently afforded by them in this distressing malady. It seems not improbable that the contractility of the bronchial tubes may serve to regulate the supply of air to the lobules, in accordance with the wants of the system, just as the contractility of the minute arteries regulates the supply of blood to the organs to which they proceed; and it may possibly be through this channel that the remarkable variation is effected in the amount of respiration, which adapts the quantity of heat produced to the depression of the external temperature. It has been further suggested by Dr. W. T. Gairdner,* that the contractility of the smaller bronchi may serve to expel collections of mucus which have accumulated in them, and which neither ciliary action nor the ordinary expiratory efforts suffice to displace.

264. The elasticity of the lungs, which in many animals, as the horse, is remarkably increased by the dense layer of elastic tissue by which they are invested,† plays an important part in the respiratory acts. Donders‡ estimates the expiratory force derived from the elasticity and muscular tension of the lungs, and coming into play in ordinary respiration, as equal to a pressure of about 5 ozs. on the square inch; but the elastic tension is rapidly increased by the dilatation of the lungs with air, and the carefully-conducted experiments of Dr. Hutchinson§ led him to estimate it at certainly not less than 8 ozs. upon each square inch of surface when the lungs have been filled by the deepest possible inspiration; so that its whole amount (reckoning an average surface of 300 sq. in. for the male, and 247 sq. in. for the female) will be not less than 150 lbs. for the male, and 123½ lbs. for the female. This force is exerted in aid of the *ex*piratory movement, and is directly antagonistic to the *in*spiratory;‖ so that the inspiratory muscles must overcome it, in order to produce complete distension of the pulmonary cavities. This distension is entirely accomplished by the action of the muscles external to the thorax, or partly forming its parietes.

Rosenthal ("Die Athembewegungen," p. 232), Rugenberg ("Studien des Phys. Institut zu Breslau," 1863, p. 47) and Wintrich ('Krankheit. d. Resp. Org.' in Virchow's "Handbuch der Pathol.," 1855–57) maintain that if a manometer be inserted into the trachea, irritation of the peripheric extremity of the Vagus never produces any increase of pressure, which would certainly occur if the capacity of the bronchi diminished.

* "Edinburgh Monthly Journal," May, 1851.

† See G. Gulliver's Note to Willis's Translation of "Wagner's Physiology," 1844, p. 360.

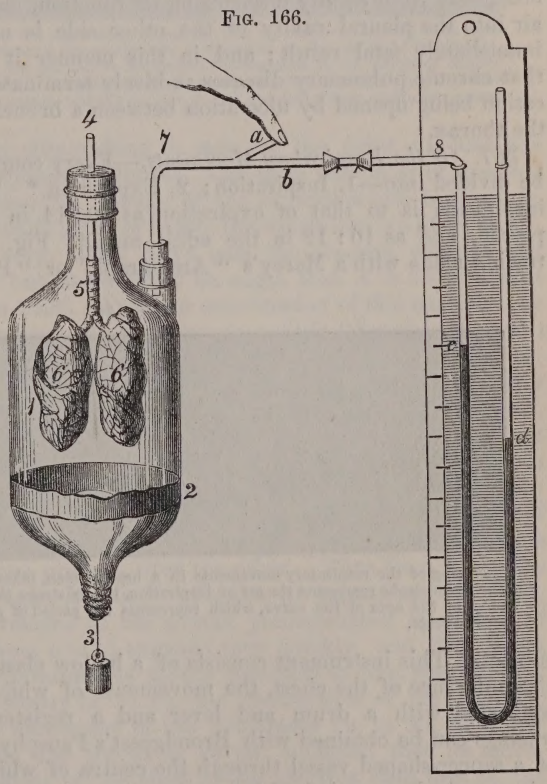
‡ See his Essays in Henle and Pfeuffer's "Zeitsch.," Band iii. and iv.

§ "Cyclop. of Anatomy," Art. 'Thorax,' vol. v. p. 1058.

‖ Thus being directly opposed to the action in birds.

265. The mechanism of the respiratory acts may be rendered clearly intelligible by the accompanying diagram, in which the trachea and lungs (5, 6, Fig. 166) are enclosed in a glass vessel with three openings. The lower opening (2) is closed by a bladder or piece of caoutchouc, representing the diaphragm, and capable of being either pushed into the cavity of the vessel or of being drawn down by a weight. The upper opening is closed by a cork, through which a glass tube (4), firmly attached to the trachea, passes. The lateral opening (7) is connected with a manometer (*c*, *d*) by a tube (*b*), having a small lateral branch (*a*) opening to the air. If the openings (*a* and 4) be now stopped whilst the bladder is extended by the weight (3), the rarefaction of the air in the glass vessel will be made apparent by the rise of the mercury in the arm (*c*) of the manometer. It is obvious that the pressure of the air within and without the lungs will be different, and consequently, on opening the orifice of the tube (4) air will rush through it and the trachea to equalise the pressure as far as the elasticity of the lung will permit. Such, with the exception that in the living body no air intervenes between the surface of the lung and the walls of the thorax, and therefore no rarefaction, but only a tendency to a vacuum occurs, are the conditions present in the ordinary act of inspiration. On the contrary, with the same exception, the act of expiration may be imitated by pushing the bladder into the vessel; for then the pressure on the exterior of the lungs will be increased, the mercury in the arm (*c*) of the manometer will descend, and, aided by their own elasticity, for the lungs are always on the stretch, they will contract upon and drive out the air contained within their cavities.

Fig. 166.



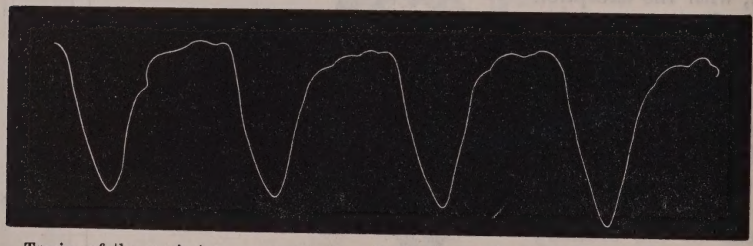
Apparatus constructed by Donders to show the Mechanism of Respiration.

266. The complete dependence of the expansion of the Lungs upon the enlargement of the cavity of the chest is well shown by the effect of admission of air into the pleural cavity. When an aperture is made on either side (as by removing the finger from the orifice of the tube *a* in the apparatus represented in Fig. 166), so that the air rushes in at each inspiratory movement, the expansion of the lung on that side is diminished, or entirely prevented, in proportion to the size of the aperture. If air can enter through it more

readily than through the trachea, an entire collapse of the lung takes place; and by making such an aperture on each side, complete asphyxia is produced. But if it be too small to admit the very ready passage of air, the vacuum produced by the inspiratory movement is more easily filled by the distension of the lungs than by the rush of air into the pleural cavity; so that a sufficient amount of change takes place for the maintenance of life. This is frequently observed in the case of penetrating wounds of the thorax, in the surgical treatment of which it is of great importance to close the aperture as completely as possible; when this has been accomplished the air that had found its way into the cavity is soon absorbed, and the lung resumes its full play. Where one lung is obstructed by tubercular deposit, or is prevented in any other way from rightly discharging its function, an opening that freely admits air into the pleural cavity of the other side is necessarily attended with an immediately fatal result; and in this manner it not unfrequently happens that chronic pulmonary diseases suddenly terminate in Asphyxia, a communication being opened by ulceration between a bronchial tube and the cavity of the thorax.

267. *Of the Respiratory Movements.*—Every complete act of respiration may be divided into—1, Inspiration; 2, Expiration.* The duration of the act of inspiration is to that of expiration as 10 : 14 in the child, female, and old person, and as 10 : 12 in the adult male.† Fig. 167 represents a normal tracing made with a Marey's "Atmograph" or "Pneumograph" in a healthy

FIG. 167.



Tracing of the respiratory movements in a healthy man, taken by M. Marey's Pneumograph. The down-stroke represents the act of inspiration, the up-stroke that of expiration. The undulations at the apex of the curve, which represents the period of *pause* of Longet, are due to the cardiac beats.

subject. This instrument consists of a hollow elastic cylinder applied to the circumference of the chest, the movements of which it follows. The tube is connected with a drum and lever and a registering apparatus. Similar tracings can be obtained with Brondgeest's Pansphygmograph, which consists of a saucer-shaped vessel through the centre of which a hole is bored, and a tube attached connected with a registering apparatus. The vessel is covered with a double layer of caoutchouc between which a sufficient quantity of air is introduced to cause it to be slightly prominent. This is applied firmly, by means of bands to the chest-wall, and the movements of the chest are then easily registered. A minute investigation of the variations of pressure in ordinary respiration has been made by Ewald with a specially modified manometer, and the accompanying diagram represents an analysis of a normal

* The pause which was admitted by Vierordt and others to occur between Expiration and Inspiration, has been shown by Riegel (Wurzburg. "Med. Gesell.," Band vii. 1867, p. 321), with a self-registering apparatus, not to be present, at least when the body is in a horizontal position.

† Sibson, "Med.-Chir. Transact.," vol. xxxi., and "Medical Anatomy."

espiratory pressure curve. In the first place the very regular transition of nspiration into expiration may be observed. The line D to F crossing the abscissa without the slightest notch or indent, which can only result from the

FIG. 168.

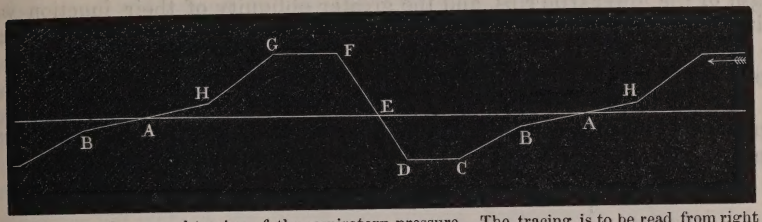


Diagram of a normal tracing of the respiratory pressure. The tracing is to be read from right to left. The part below the horizontal line or abscissa corresponds to the period of inspiration, and indicates negative pressure; the part above the abscissa corresponds to the period of expiration, and indicates positive pressure. The point where the curve cuts the abscissa is the moment where inspiration passes into expiration, and the point A is the moment where expiration passes into inspiration.

inspiratory pressure steadily diminishing to zero (at the point E), and the expiratory pressure rising equally uniformly. The same regularity is observed in the line H to B, representing the passage of the expiration into inspiration. This takes place more gradually; that is to say, the expiration is a little longer, but in exactly the same way. The curve cuts the abscissa without any indent, as a straight line, but at so slight an angle that it is often almost coincident with the abscissa itself. From an examination of this curve it may further be seen that the period of expiration is a little (though not much) longer than that of inspiration, the proportion being about as 12 : 11. Inspiration begins very gradually, the cavity of the chest increasing most rapidly at the end of the second third of the inspiratory period. On the other hand, in expiration the pressure is greatest at the end of the first third, and then gradually diminishes. Two nearly symmetrical indents, B and H, are seen in the ascending and descending curves. These Ewald regards as an expression of the fact that the chest cavity is more rapidly dilated by the movements of the thorax than by the contraction of the diaphragm. These two movements are indeed combined, but one prevails over the other. Thus from A to B the contraction of the diaphragm is chiefly effective in expanding the chest, whilst from B to E the movement of the thorax predominates, by means of which the thorax first (from B to C) expands very quickly, and then (from C to D) more slowly. In expiration the thorax contracts at first very quickly (from E to F), then more slowly (F to G), the contraction of the thoracic walls first acting, and the movement of the diaphragm (H to A), then first becoming perceptible, when the thorax is so far collapsed that its movement in diminishing the cavity of the chest is less effective than that of the diaphragm. In ordinary tranquil breathing (especially in children), the action of the diaphragm is alone nearly sufficient to produce the necessary exchange of air, and this muscle is consequently the chief inspiratory agent; but when a full inspiration is required, the cavity of the chest is dilated laterally and antero-posteriorly, as well as inferiorly.* The enlargement of the chest in both these directions is effected by the elevation of the ribs; for whilst, in the undilated state of the thorax, the ribs form an angle with their cartilages,

* Bert ("Leçons," p. 352) has clearly shown by tracings with his "Tambour pour recueillir les Mouvements du Thorax," or Pneumograph, that in the dog the diaphragm in contracting causes the 6th and lower ribs to rise, and thus to increase the transverse diameter of the chest; whilst, on the contrary, the 5th and upper ribs tend to descend and diminish the transverse diameter.

which become less and less obtuse as we pass from the first rib downwards, the elevation of the ribs tends to bring them and their cartilages more nearly into a line, and thus separates them more widely from the median plane, and at the same time causes them to push forward the sternum. Owing to the greater length of the lower true ribs, and the greater obliquity of their junction with their cartilages, both these changes are more considerable in the lower part of the thorax than in the upper; and this is especially the case in adult men, whose respiration has been designated as "inferior costal," whilst in females the mobility of the first rib and of the whole of the upper part of the thorax is greater, so that their respiration may be designated as "superior costal."—The respiratory muscles and nerve-supply are as follows:—

	Inspiration.		*Expiration.*	
Quiet breathing	Diaphragm.	Phrenic.	Elasticity and weight of the thorax and lungs.	
	Ext. intercostal.*	Intercostal nerves.		
	Levatores costarum.			
	Serratus posticus superior.	Cervical and brachial plexuses.		
	Three scaleni.			
Forced or laboured breathing	Sterno-mastoid.	Cervical and brachial plexuses.	Serratus post. inf.	Dorsal and Lumbar nerves.
	Trapezius.		Latissimus dorsi.	
	Pectoralis minor.		Intercost. interni.	Intercostal nerves.
	Rhomboidei.		Triangularis sterni.	
	Serratus anticus major.		Rectus abdominis.	Abdominal branches of Intercostal nerves.
	Serratus posticus superior.	Dorsal nerves.	Obliqui „	
	Extensors of the spine.		Transversus „	
	Sterno-hyoid.	Hypoglossal.	Quadratus lumborum.—Lumbar plexus.	
	Sterno-thyroid.			
	Crico-arytenoid post.	Recurrent laryngeal.		
	Thyro-arytenoid.			
	Dilatator narium.	Facial.		
	Levator alæ nari.			
	Levator uvulæ.			
	Levator palati.	Facial.		
	Azygos uvulæ.			

* Hutchinson, Op. cit., p. 1055. See also Cleland, "Journal of Anat. and Physiol.," vol. i. 1867, p. 209. There is probably no point in the whole range of physiology respecting which such different opinions have been entertained by good observers as upon the action of the intercostal muscles, and it may be instructive to give the following enumeration of them, drawn from Beau and Massiat ("Archiv. Gén. de Méd.," 1842), Küss ("Physiologie," 1873, p. 343), Budge ("Compendium de Physiol. Humain," 1874, p. 55), and Colin ("Traité de Physiologie Comparée," 1873, p. 251, *et seq.*:—1. Both the external and internal intercostals are *inspiratory muscles* (Borelli, Senac, Boerhaave, Winslow, Haller, Cuvier, Colin, Wündt, Duchenne, Duval); Duchenne supports his opinion by reference to a case in which all the respiratory muscles were paralysed except the intercostals, and yet in which respiration was maintained; Duval rests his upon experiments made on decapitated criminals shortly after death. 2. Both sets of muscles are *expiratory* (Vesalius, Diemerbröck, Sabatier, Beau and Massiat, Longet). This view rests on the fact that in vivisections the muscles may be seen to contract in forced expiration, as in coughing or crying out. Moreover, the intercostals are present in Birds, in which the act of expiration alone is due to muscular effort. 3. The *external* intercostals are *expiratory;* the *internal, inspiratory* muscles (Galen, Bartholinus). 4. The *external* intercostals are *inspiratory;* the *internal, expiratory* muscles (Spigelius, Vesling, Hamberger, and, with some modification, Sibson, Hermann, Cleland, and Foster). According to Sibson the external intercostals are inspiratory, except at their anterior part, in the five inferior intercostal spaces; the internal intercostals are inspiratory in the anterior part of the five first spaces, but have elsewhere an expiratory action. Hermann observes that the external muscles are *inspiratory* where they are attached to the osseous portions of the ribs, the internal where attached to the cartilaginous portions; but as this corresponds to the chief action of the two sets of fibres both may be regarded as inspiratory muscles. Cleland (Letter to Editor) remarks similarly that the external and anterior fibres of the internal intercostal are most advantageously disposed for elevating the ribs, and that the remaining intercostals are most advantageously placed for depressing the ribs; but that all the intercostals are capable of giving some assistance in inspiration, as also in forced expiration, whilst ordinary expiration is accomplished altogether by elasticity, and not by muscular effort at all. Aeby ("Lehrbuch," 1871, p. 379) holds that both sets of muscles approximate the adjoining ribs, but whether this occasions an elevation or depression of the whole series is dependent on the coincident action of other muscles. 5. Mayo and Magendie,

The movements of the heart have a slight influence on the lungs, the systole aiding inspiration, the diastole expiration.*

268. The *extent of movement* of the several parts of the chest during the respiratory acts may be registered by an instrument suggested by Dr. Burdon Sanderson,† and named by him the 'recording stethometer.' From experiments made with this instrument he finds that in the ordinary respiration of a healthy, muscular, young man, aged twenty-two, the upper antero-posterior diameter, which was equal to 146 mm., varied one mm.; the lower sternal diameter, which equalled 203 mm., varied 1·5 to 1·8 mm.; and the transverse costal diameter at the level of the eighth rib, which equalled 228 mm., varied 1·7 to 2·0 mm. In forced respiration the variations of the antero-posterior diameters of the upper part of the chest were much more extensive, the ends of the upper ribs moving horizontally forward—*i.e.*, in a plane parallel to the middle plane of the body, from 12–30 millimetres: the advance of the third rib being greater by several millimetres than that of the fifth, and this Dr. Ransome attributes to an actual straightening of the ribs.‡ The following Table, based on Riegel's experiments, gives the relative movement of the different points of the front of the chest in six men and six women, and shows well the contrast between the sexes:—

MAN.	Manub. Sterni.	Corp. Sterni.	Process. Ensif.	Epigast.
I.	1	1	1·5	4·5
II.	1	1	1·1	6·6
III.	1	1·3	10·0	12
IV.	1	1·8	3·7	11·4
V.	1	1·2	1·5	6·8
VI.	1	1·1	1·8	7·2
WOMAN.				
I.	1·8	1·1	1	0·73
II.	1·5	1·2	1	0·63
III.	1·4	1·3	1	1·5
IV.	5	3·1	1	1·9
V.	1·1	1	1	1·6
VI.	3·8	2·5	1	1·8

The extent of the respiratory movements is affected by various morbid conditions. Thus, when dislocation of the spine takes place above the origin of the intercostal nerves, but below that of the phrenic, so that the former are paralysed, the respiratory movement is confined to the diaphragm: this is insufficient, and with the coincident paralysis of the vaso-motor nerves leads to the effusion of serum into the lungs, and slow asphyxia, which usually proves fatal in a few days. Even where the muscles and nerves are all capable of action, the full performance of the inspiratory movements may be prevented by the solidification or engorgement of any part of the lung which interferes with its free distension; or by adhesions between the pleural surfaces, which offer a still more direct impediment. When these adhesions are of long stand-

and Volkmann ("Centralblatt," 1877, p. 115) regard both sets of muscles as at once expiratory and inspiratory in their action. Lastly, Van Helmont, Arantius, Cruveilhier, Küss, and Jobelin consider that both sets of muscles are passive in the movements of respiration, and simply form an immovable wall to the chest, or rather they contract, not to produce the movements of inspiration or expiration, but to resist at both periods the pressure either of the external or of the internal air.

* See Voit and Lossen, "Zeitschrift für Biologie," Band i.; Ceradini, "Verhand. des natur.-hist.-med. Vereins zu Heidelberg," 1869. Also Landois, who, however, holds a different opinion ("Berlin Klin. Wochens.," 1870).

† "Handbook for the Physiological Laboratory," p. 291.

‡ See Arthur Ransome, 'On the Mechanical Conditions of the Respiratory Movements in Man,' "Proceed. Roy. Soc.," Nov. 1, 1872.

ing, they are commonly stretched into bands, by the continual tension to which they are subjected. If the impeding cause affect both sides, the movements of both will be alike interfered with; but if one side only be affected, its movements will be diminished, whilst those of the other remain natural; and the physician hence frequently derives an indication of great value in regard to the degree in which the lung has become incapable of performing its functions. It is to be remembered, however, that the action both of the diaphragm and of the elevators of the ribs may be prevented by pain, either in the muscles themselves or in the parts which they move; thus the descent of the diaphragm is checked by inflammation of the abdominal viscera or of the peritoneum; and the play of the intercostals by rheumatism, pleurisy, pericarditis, or other painful disorders of the parts forming the parietes of the thorax. In man the acts of respiration are properly effected through the nostrils, which are lined by a highly vascular membrane kept constantly moist by numerous glands, and by the lachrymal secretion, whilst its surface is greatly extended by the sinuosities of the turbinal bones. The inspired air is thus rendered moist and warm before reaching the sensitive larynx and lungs, and the coughs and colds so prevalent in this country in the winter and spring months might often be avoided if care were taken, especially on sudden exposure to cold air, to breathe through the nostrils instead of the mouth. The passage of air into and from the lungs is accompanied by a peculiar soft blowing sound, termed the *respiratory murmur* or *bruit*. The act of inspiration being more rapid and energetic than that of expiration is attended by a louder sound, which is most distinctly audible in young children and in thin persons. It probably arises either, as Dr. Salter* suggests, from the current of air striking against the angles of division of the bronchia, or as indicated by Dr. Waters,† from a slight constriction that exists at the mouth of each air-sac. Other causes that have been assigned to it are the separation of the moist septa of the alveoli, the general friction of the air against the walls of the bronchial tube, and the reverberation of the glottidean bruit (Sabatier; Cornil, 1873). The expiratory murmur is exclusively due to the friction of the air against the glottis (Chauveau).‡

269. The relative amount of muscular force which is required for the two respiratory movements respectively is affected in a very remarkable manner by the elasticity of the walls of the thoracic cavity and of the lungs themselves; for this (like the elasticity of the lungs) supplies a force which greatly aids the *ex*piratory movement, whilst it offers a corresponding opposition to the *in*spiratory. Here, also, the degree of force exerted increases very rapidly with the degree of distension. Thus, in a body experimented on by Dr. Hutchinson,§ the following were the relations between the amount of air forced in, the resisting elasticity, as shown by the height of mercury supported, the actual pressure upon each square inch of surface which this indicated, and the total pressure over the surface of the chest, reckoning its area at 206 square inches:—

Cubic inches.				*Pressure in height of Mercury.*	*Pressure per sq. in.*	*Total pressure.*
Air forced in	70	Resisting elasticity		1·00 inch.	7·8 oz.	104·4 lbs.
„	90	„	„	1·50 „	11·7 „	150·6 „
„	180	„	„	3·25 „	25·3 „	326·3 „
„	200	„	„	4·50 „	35·1 „	451·9

To this 451·9 lbs. must be added at least 128 lbs. for the elastic force of the lungs themselves at that degree of distension, making altogether 580 lbs.; and

* Pamphlet on "Cause of Respiratory Murmur," 1864. † "Med.-Chir. Rev.," 1865, p. 217.
‡ See Budge, "Compendium de la Physiologie," 1874, p. 69. § Op. cit., p. 1056.

as the subject of this observation could expire during life considerably more air than the highest amount forced into his chest after death, there can be little doubt (judging from the rapid ratio in which the elastic force increases when the distension is approaching its limits) that the muscular power required to overcome this, towards the close of a very deep inspiration, could not have been less than 1000 lbs. The co-operation of the elastic resistance with the expiratory movement, and its antagonism to the inspiratory, is doubtless the principal cause why the power of the expiratory muscles, as tested by the height of the column of mercury supported by the air, should always be greater than that of the inspiratory muscles;* and why the expiratory power should be very much greater when the chest has been well filled with air, than when it is comparatively empty. The following is given by Dr. Hutchinson as the range through which these powers may vary within the limits of health:—

Power of Inspiratory Muscles.		*Power of Expiratory Muscles.*
1·5 inch.	Weak	2·0 inches.
2·0 „	Ordinary	2·5 „
4·5 „	Remarkable	5·8 „
7·0 „	Very extraordinary	10·0 „

Lassar† gives nearly similar numbers. Other observers have, however, found the pressure exerted in inspiration and expiration to be much less. Valentin‡ stated it at 1-5th inch, Hg for ordinary inspiration and expiration; with quite tranquil respiration the numbers were – 4·0 and + 3·6 mm. Hg. Donders§ estimated it at – 3 mm. Hg for inspiration, and about 2 mm. Hg for expiration; and Ewald,‖ the latest writer, with improved methods, estimates the normal pressure in quiet breathing to be only 0·1 mm. Hg for inspiration and 0·13 mm. Hg for expiration. The expiratory power may be augmented by the habitual performance of movements in which they participate; and thus the inspiratory power is the preferable test of the *vis vitæ*. This has been found by Dr. Hutchinson to bear some relation to height, being greatest (on an average of a considerable number of cases) when the stature is 5 feet 7 or 8 inches; and diminishing above that height, as well as below it. Fick estimates that the work accomplished in effecting the inspiration of 600 c.c. is equivalent to 0·63 kilogrammetre, and Prof. Haughton estimates the daily work of the respiratory muscles at 21 foot-tons.¶

270. It is impossible to form a correct estimate, by observations on one's-self, of the usual number and extent of the respiratory movements; since the direction of the attention to them is certain to increase their frequency and amount. In general it may be stated, that from 16 to 20 alternations usually occur in a minute;** of these, the ordinary inspirations involve but little movement of the thorax; but a greater exertion is made at about every fifth recurrence. According to Quetelet, the infant at birth breathes—

	44 times per minute.
At 5 years of age	26 „
„ 15 to 20	20 „
„ 20 „ 25	18·7 „
„ 25 „ 30	16 „
„ 30 „ 50	18·1 „

The average numerical proportion of the respiratory movements to the pulsa-

* See Dr. Hutchinson, Op. cit., p. 1061.

† Lassar, "Zur Manometrie der Lungen Inaug-abhand. Wurzburg," 1872.

‡ "Physiology," translated by Brinton, 1853, p. 235.

§ Donders, "Zeitschrift f. Rational. Med.," Band iii.; Krahmer, Haeser's "Archiv," 1847, Band ix.

‖ J. R. Ewald, Pflüger's "Archiv," Band xix. 1879, p. 461.

¶ Lecture delivered at the Meeting of Brit. Med. Assoc. at Oxford, August, 1868.

** See Dr. Hutchinson's Table, in "Cyclop. of Anat. and Phys.," vol. iv. p. 1085.

tions of the heart is about 1 : 5, 1 : 4½, or 1 : 4; and when this proportion is widely departed from, there is reason to suspect some obstruction to the aëration of the blood, or some disorder of the nervous system.* Thus in Pneumonia, in which a greater or less amount of the lung is unfit for its office, the number of respirations increases in a more rapid proportion than the acceleration of the pulse; so that the ratio becomes as 1 to 3, or even 1 to 2, in accordance with the degree of engorgement.† In Hysterical patients, however, a similar increase, or even a greater one, may take place without any serious cause; thus Dr. Elliotson‡ mentions a case in which the respiratory movements of a young female, through a nervous affection, were 98, or even 106, whilst the pulse was 104. On the other hand, the respiration in certain typhoid conditions and in narcotic poisoning becomes abnormally slow, owing to the torpid condition of the nervous centres, the proportion being 1 to 6, or even 1 to 8; and in such cases the lungs not unfrequently become œdematous, from a cause hereafter to be mentioned. M. Marey§ believes it may be shown that the frequency of the respiratory acts are, as in the analogous case of the heart, almost always diminished, whilst they are at the same time rendered deeper by the existence of any obstacle to their due performance; so that there is an evident attempt made to effect, within certain limits, the introduction of the same quantity of air into the lungs in a given time; and in an ingenious instrument he has devised, where, by the reversal of a valve, difficulty of breathing may be induced either during inspiration or expiration, he has observed that that act is prolonged in which the dyspnœa is made to occur.

271. We have now to inquire into the mode in which the muscular movements of respiration are kept up by nervous power. Though to some extent under the control of the Will, they are partly 'automatic' and partly 'reflex' in their nature. Their chief centres are placed on either side of the apex of the *calamus scriptorius*, being in close relation with, or forming part of, the nuclei of origin of the Pneumogastric nerves, which are the principal excitor nerves that convey the stimuli on which the reflex movements are dependent, whilst from the adjacent parts of the medulla oblongata and spinalis proceed the chief motor nerves by which they are carried into effect. The whole of the Encephalon may be removed from above, and the spinal cord (as far up as the origin of the phrenic nerve) from below without suspending the most essential of the respiratory movements; yet the destruction of these centres causes their immediate cessation, and as the arrest of respiration is incompatible with life, they were named by Flourens the 'noeud vital.' It is uncertain whether there are distinct centres for the expiratory and for the inspiratory muscles, but there is reason to believe that a respiration-regulating centre lies beneath the corpora quadrigemina.‖ The experience of every one informs him that the Respiratory movements are partly

* V. Ghert has shown that, during violent exertion, the respirations increase in frequency more than the pulsations; but that in the subsequent period of rest, the increased activity of the cardiac movements is more persistent than that of the respiratory. For a list of the number of Respirations per minute in a great number of different animals see P. Bert, "Leçons," p. 393, *et seq.*

† See a Paper by Dr. Hooker, an abstract of which will be found in the "British and Foreign Medical Review," vol. iv. p. 263. ‡ "Physiology," p. 215, *note.*

§ "Mémoires de la Soc. de la Biologie," 1865, p. 175. Bert ("Leçons," p. 410) shows that many statements, though accurate when the obstacle to respiration is slight, must be accepted with some reservation when the obstacle is great, the amplitude then decidedly diminishing.

‖ Dr. Martin and Booker, Foster's "Journal of Physiology," vol. i. 1878–79, pp. 131 and 170.

under the control of the will, though frequently unrestrainable by it. In ordinary circumstances, when the blood is being perfectly aërated, and there is a sufficient amount of arterial blood in the system to carry on the functions of life for a short time, we can suspend the respiratory actions during a few seconds without any inconvenience. If, however, we endeavour to prolong the suspension, the stimulus occasioned by the circulation of venous blood through the respiratory centres, and that conveyed by the excitor nerves to the Medulla oblongata, becomes too strong, and we cannot avoid making inspiratory efforts; and if the suspension be still further prolonged, the whole body becomes agitated by movements which are almost of a convulsive nature, and no effort of the will can then prevent the ingress of air.* It is easy to understand why, in the higher animals at least, and more especially in Man, the respiratory actions should have become thus placed under the direction of the will: since they are subservient to the production of those Sounds by which individuals communicate their feelings and desires to each other; and which, when articulate, are capable of so completely expressing what is passing in the mind of the speaker. The respiratory centres are, moreover, as Duchenne† has pointed out, in immediate contiguity to the hypoglossal nucleus governing the movements of the tongue; to the inferior nucleus of the facial, regulating the movements of the lips; and to the nucleus from which the cardiac branches of the spinal accessory and pneumogastric nerves arise, so that all these functions are brought into immediate relation with the respiratory acts; and in the disease known as glosso-labio-laryngeal paralysis these centres are affected successively, the tongue being first attacked, then the muscles of the palate, then the orbicularis oris, whilst the fatal termination of the disease is preceded by attacks of suffocation. That the respiratory movements, as ordinarily performed, are essentially independent of the Will, appears not only from our own consciousness, but also from cases of paralysis; in some of which the power of the will over the muscles has been lost, whilst the movements have been kept up by the automatic or reflex action of the respiratory ganglia; whilst in others, some of the respiratory muscles have been motionless during ordinary breathing, and yet have remained under the power of the will.‡ That consciousness is not a necessary link in the chain of causes which produce the respiratory movements, we are enabled to judge from the phenomena presented by the human being in sleep and coma, by anencephalous fœtuses, and by decapitated animals. This conclusion is confirmed by a case recorded by Dr. H. Ley,§ who had under his care a patient in whom the pneumogastrics appeared to be diseased; the lungs suffered in the usual way in consequence, and the patient had evidently laborious breathing; but he distinctly said that he felt no uneasiness in his chest. The *automatic* activity of the respiratory centres is excited by the circulation of venous blood through the vessels of the medulla oblongata,‖ the

* It is asserted by M. Bourdon ("Recherches sur le Mécanisme de la Respiration," p. 21) that no person ever committed suicide, though many have attempted to do so, by simply holding the breath; the control of the will over the respiratory muscles not being sufficiently great to antagonise the stimulus of the "besoin de respirer," when this has become aggravated by the temporary cessation of the action. But such persons have succeeded better by holding the face beneath the surface of water; because here another set of muscles is called into action, which are much more under the control of the will than are those of respiration; and a strong volition applied to these can prevent all access of air to the lungs, however violent may be the inspiratory efforts.

† Duchenne, "De l'Electrisation localisée," 1872.

‡ Such cases are mentioned by Sir C. Bell, in the appendix to his work on the "Nervous System of the Human Body."

§ "On Laryngismus Stridulus," p. 417.

‖ See Rosenbach, "Centralblatt f. d. Med. Wiss.," 1877, p. 96.

real stimulus appearing to be a deficiency in the amount of oxygen supplied, though perhaps the presence of an excess of CO_2 in the blood may constitute an additional stimulus.*

272. The *reflex*, as opposed to the automatic activity of the respiratory centres is chiefly excited through the *Vagi* or Pneumogastric nerves, and especially through the branches of these nerves distributed to the larynx and lungs. Other sensory nerves, however, as the fifth, and the sensory nerves of the skin generally, may convey impressions which are reflected at the medulla to the muscles maintaining respiration; painful impressions usually leading to expiratory efforts, whilst slighter degrees of stimulation cause inspiratory movements. Under ordinary circumstances—that is to say, in tranquil breathing—it would appear that the deficiency of oxygen or the accumulation of carbonic acid and other products of disintegration in the blood acts as a stimulus alike to the vagal centres and to the sentient extremities of the Vagus distributed to the lungs. In the latter case the excitation is conveyed through the trunks of these nerves to the vagal centres in the medulla oblongata, from whence impulses are liberated which descend through the spinal cord and chiefly through its lateral columns† to the phrenic nerves, which causing the diaphragm to contract, an act of inspiration takes place. The Blood, now become oxygenated, ceases to be a stimulus to the vagal nuclei and nerves, the vagal centres become quiescent, the diaphragm relaxes, and the elasticity of the chest and lungs expels the air, and the act of expiration is effected.‡ The succession of these phenomena constitutes *Eupnœa* or normal respiration, but if from any circumstances, as the performance of active exercise, or exposure to a high temperature,§ the consumption of oxygen and production of carbonic acid are increased, the vagal centres and extremities are more strongly excited, they initiate more powerful impulses, and other motor nerves (such as the intercostals) besides the phrenics are excited. In cases where the blood is still less perfectly arterialised, as when the supply of air is insufficient, the vagal centres are still more strongly excited, and all the accessory muscles are then called into play. If an animal be made to breathe superoxygenated air, or if its blood be surcharged with oxygen by the vigorous performance of artificial respiration, the respiratory movements gradually cease, and the condition termed *apnœa* is established.‖ This state only lasts for a short period, and respiration again commences. Considerable difference of opinion exists in regard to the cause of apnœa, some¶ considering it to be due to the quiescence of the respiratory centres, which being well supplied with oxygen liberate no impulses to the respiratory muscles, whilst others** maintain that it is essentially due to muscular exhaustion, occurring only when the subject of the experiment is much distressed, and

* Formerly the presence and accumulation of CO_2 in the blood were believed to constitute the stimulus to the centres of respiration. Nasse maintained that a deficient supply of oxygen constitutes a stimulus, by causing the central ganglia to respond more readily to the ordinary and *à fortiori* to any extraordinary quantity of CO_2 in the blood, whilst their excitability is lowered when the proportion of oxygen in the blood circulating through them is increased.

† See Schiff, Pflüger's "Archiv," Band iv. p. 225.

‡ Breuer, "Sitz. d. Wien. Akad.," 1868, Heft xii., attempts to show that the mere act of inspiration leads to relaxation of the respiratory muscles, and is a stimulus to the nerves supplying the expiratory muscles, and *vice versâ*.

§ See Goldstein, "Verhandlung Phys. Med. Gesell. zu Würzburg," Band ii. 1871, p. 156.

‖ See the experiments of Czermak, "Centralblatt," Jan. 3rd, 1866; Pflüger, "Pflüger's Archiv," 1868, p. 61; Schwarz, "Beiträge."

¶ Rosenthal, "Comptes Rendus," 1861, p. 754.

** As Hoppe-Seyler, "Zeits. f. Physiol. Chemie," Band iii. 1879, p. 109; and Rosenbach, "Centralblatt. f. d. Med. Wiss.," 1877, p. 96.

after its respiratory movements have become irregular. Hoppe-Seyler observes that the duration of the apnœa, when it lasts one minute or more, is far more than sufficient to reduce the blood to its ordinary condition as regards oxygen; he points out also that arterial blood is naturally saturated with oxygen, and maintains that respiration in oxygen or in compressed air causes little difference in the frequency or depth of the respiratory acts. Rosenbach explains the phenomenon of apnœa by referring it to inhibition of the respiratory movements, owing to the mechanical stimulation of the pneumogastric nerves in the process of artificial respiration, these nerves exerting a constricting influence on the vessels of the medulla oblongata, whereby the liberation of impulses to the inspiratory muscles is diminished. Perhaps we may admit two kinds of apnœa, one of which is due to slight increase in the amount of oxygen in the blood, whilst the other is attributable partly to contraction of the vessels of the medulla oblongata, caused by stimulation of the vagus, which prevents the liberation of motor impulses to the muscles of respiration. It is certain that apnœa may be observed in those who are performing, or who have first performed, some violent exertion, and it here undoubtedly appears to result from exhaustion of the respiratory muscles.

273. When the movements of respiration are performed with difficulty and unusual effort, *Dyspnœa* is said to exist. This condition may be established as a result either of a deficient supply of oxygen or of accumulation of CO_2 in the blood. Both conditions induce dyspnœa, and in addition cause increase of blood pressure and diminished absorption of oxygen; but the toxic influence of CO_2 is especially characterised by a reduction of the amount of CO_2 eliminated, and by rapidly supervening paralysis of the motor and sensory nerve centres; whilst a deficient supply of oxygen occasions violent convulsions shortly before death.* Dyspnœa from deficiency of oxygen can be produced by the inhalation of Nitrogen or Hydrogen; in such cases Pflüger has shown the oxygen is greatly diminished, whilst the carbonic acid is not materially increased, or may even be diminished.† Dyspnœa from excess of carbonic acid can be induced by making the animal breathe air surcharged with that gas, or by preventing its elimination from the system. Traube‡ produced dyspnœa by making an animal breathe a mixture of 28 per cent. of carbonic acid gas, 32 per cent. of oxygen, and 40 per cent. of nitrogen.§ Dyspnœa produced by such gases as carbonic oxide and nitrous oxide is due apparently to these gases withdrawing oxygen from the blood, whilst phosphuretted, arseniuretted, and sulphuretted hydrogen reduce the hæmoglobin, and after first exciting rapidly paralyse the respiratory centres. Hydrocyanic and hydrochloric acid gases, chlorine, sulphurous acid, and some other gases seem both to act destructively on the blood, and to destroy the functional activity of the vagal nuclei.

274. The important part played by the Vagi in the respiratory acts may be experimentally shown by their division, and the application of a stimulus to their proximal extremities. The trunks of the vagi are not endowed with much sensibility, for if pinched or pricked the animal does not exhibit nearly such

* Friedländer and Herter, "Zeits. f. Physiol. Chemie," Band iii. 1879, p. 45.

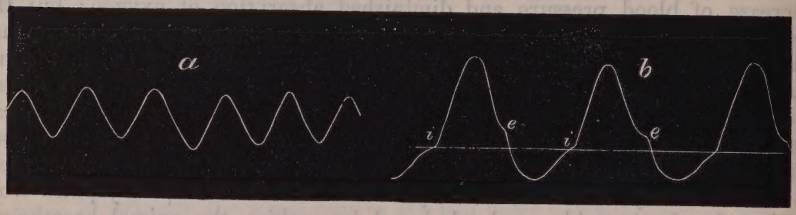
† See Pflüger's Essay in Band i. of his "Archiv," 1868.

‡ "Allgem. Med. Centralblatt," 1868, Nos. 38 and 39. See also Thiry, "Rec. des Travaux de la Soc. Méd. Allemande de Paris," 1865; and Dohmen, "Unters. aus dem Physiol. Lab. zu Bonn," 1865, p. 83.

§ M. Bert ("Séance de la Soc. de Biologie," Feb. 3rd, 1872, "Rev. Scient.," 2e sér. i. année, No. 37, 1872, p. 882) has shown that the barometric pressure to which the animal is exposed is of great importance in such experiments, in consequence of its effects on the diffusion of the gases.

acute signs of pain as when the trunks of the ordinary spinal nerves or of the fifth pair are subjected to similar treatment. It has been clearly ascertained that they contain some fibres which have the power of inducing inspiratory and others which induce expiratory movements. The effects of section of the vagi appear to differ considerably in different animals, which is doubtless in part due to the fact that in some animals, as the Cat and Dog, the vagus is united into one trunk with the sympathetic and depressor nerves, the section of the latter leading to vaso-motor complications; whilst in others, as in Man and the Rabbit, these nerves are separate. When the section is made on one side only in the Rabbit the effects are not constant,* though the respiratory acts are usually rendered slower, but if the division be made simultaneously on both sides, the number of respirations per minute, as was shown by Dr. Reid,† diminishes from 120–140 to 40–50. The mechanism of breathing is at the same time completely altered. Each respiration becomes much deeper than before, which is partly due to increased action of the diaphragm, and partly to the participation of the accessory muscles in the act of inspiration. The inspiratory acts are often rendered sudden and spasmodic, with long intervening pauses, but usually the difference is such as is expressed in the following tracing given by Dr. Burdon Sanderson in which the movements are seen to be more slowly performed, but to be much fuller and deeper. The quantity

Fig. 169.



a. Tracing of the respiratory movements of the cat. *a* before *b* after division of both vagi.

of air breathed per minute is, however, not materially altered, being as great after as before the section, the diminished frequency being compensated for by increased depth of the respiratory act. Still it is to be particularly observed that although the vigour of the respiratory movements does not appear to be materially impaired, the blood becomes more or less venous (Sanderson).‡ In dogs the simultaneous division of the two vagi usually reduces the number of the respiratory movements by one-half (Reid). In pigeons the number falls to one-eighth, whilst the depth of each inspiration is only increased as 1 : 2·5, the respiratory activity therefore being diminished to about one-third of its original amount (Rosenthal).§ The influence of the Vagi upon respiration may also be shown by the application of an electrical stimulus of moderate intensity to the central extremity of the divided nerves of one side. The effect will be observed to vary according to whether the animal is breathing naturally, or is in a state of apnœa or dyspnœa. If it be breathing naturally, or be in a state of eupnœa, the immediate effect of slight irritation is an acceleration of the respiratory movements, whilst if the stimulus be stronger temporary arrest of respiration in inspiration occurs, owing either to contraction or to relaxation of the diaphragm without the participation of the

* Gilchrist, "Med.-Chir. Rev.," 1858, vol. ii. p. 495. † Op. cit.

‡ See Sanderson's 'Chapter on Respiration' in the "Handbook to the Physiological Laboratory," 1873.

§ Rosenthal, "Comptes Rendus," 1861, p. 754.

other respiratory muscles.* If the excitation be still stronger, the respiratory movements are completely suspended, the diaphragm passing into a tetanic condition, which lasts as long as the stimulus is applied. In apnœa, when the blood is surcharged with oxygen, the effect is negative; in dyspnœa, when the blood is deficient in oxygen all the accessory muscles are brought into action, and the chest remains for a time in a state of tetanic expansion.† When the animal is depressed by chloral, and its nerves are exhausted, stimulation of the vagi, instead of being followed by contraction, is followed by relaxation of the diaphragm, which is regarded as the effect of the stimulation of the inhibitory fibres probably contained in the recurrents.‡

275. The motor power of the Respiratory nerves is exercised, however, not only on the muscles which perform the inspiratory and expiratory movements, but on those which guard the entrance to the windpipe, and also on some other parts. Between the superior and inferior Laryngeal nerves there is an important difference, which anatomical and experimental researches have now very clearly demonstrated. It appears from the very careful and satisfactory observations and experiments of Dr. J. Reid,§ that whilst the *inferior* laryngeal is the *motor* nerve of nearly all the laryngeal muscles, the *superior* laryngeal is an *afferent* nerve of extreme sensibility, conveying to the Medulla Oblongata the impressions made on its peripheral extremities. The motor endowments of the latter are limited to the crico-thyroid muscle, to which alone of all the muscles its filaments can be traced, the remainder being distributed to the mucous membrane of the larynx; and its sensibility is very evident, when it is pinched or irritated during experiments upon it. On the other hand, the motor character of the inferior laryngeal branch is shown by its very slight sensibility to injury, by its nearly exclusive distribution to muscles, and by its influence in exciting contraction of these when its separated trunk is stimulated.

276. The sensory branch of the vagus supplying the larynx possesses special attributes, which are comparable with those of the inhibitory nerves of the heart, for if moderate excitation be applied to the superior laryngeal nerve, the inspiratory movements are diminished in extent and frequency, whilst if the excitation be more energetic, arrest of respiration with some contraction of the expiratory muscles is produced (Breuer).‖ Similar effects are stated to be produced by stimulation of the inferior laryngeal nerve (Breuer) which must also be regarded as an inhibitory nerve for the respiratory movements. The superior laryngeal nerve responds much more readily to stimuli than the inferior. An inhibitory influence may also be exerted by stimulation of the nostrils—nasal branch of the infra-orbital (Schiff and Kratschmer.¶) Slight irritation of any sensory nerve augments the number of the respiratory movements (Schiff). Strong irritation diminishes (Mantegazza) or altogether arrests them, especially if the excitant be heat, when inspiration-tetanus is produced (Schiff). According to M. Bert** the arrest in the above instances may take place either in expiration or in inspiration, though it is more easily produced in expiration; coincidently with the arrest of the movements of

* See Burkart, Pflüger's "Archiv," Band xvi. 1878, p. 465.

† Burdon-Sanderson, Op. cit., p. 311.

‡ See Burkart, Pflüger's "Archiv," Band i. 1868, p. 107, and Band xvi. 1878, p. 427.

§ "Edin. Med. and Surg. Journ.," Jan. 1838; and "Anat., Physiol., and Pathol. Res.," chap. iv.

‖ "Sitz.-ber. d. Wien. Akad.," 1868, No. xii.

¶ "Sitz. d. k. Akad. zu Wien.," 1870, Band lxii. p. 166. See also Knoll, idem., Band lxviii. 1874.

** Brown-Séquard, "Archives de Physiologie," t. ii. pp. 179 and 322.

respiration the general movements of the animal are arrested—it remains perfectly motionless.*

277. There can be no doubt, then, that the superior and inferior laryngeal branches constitute the circle of incident and motor nerves, by which the aperture of the glottis is governed, and by which any irritation of the larynx is made to close the passage, so as to prevent the entrance of improper substances; whilst the superior laryngeal nerve also excites the muscles of expiration, so as to cause the violent ejection of a blast of air, by which the offending gas, fluid, or solid may be carried off. The effect of carbonic acid in causing spasmodic closure of the glottis is well known, and affords a beautiful example of the protective office of this system of nerves.—The mucous surface of the trachea and bronchi appears, from the experiments of Valentin, to be endowed with excitability, so that stimuli applied to it produce expiratory movements; and this evidently operates through the branches of the pneumogastric distributed upon the membrane. Here, as elsewhere, we find that a stimulus applied to the *surface* has a much more decided influence than the irritation of the *trunk* of the nerve supplying it.

278. The importance of moderate excitation of the general sensory nerves of the surface, and especially of the fifth pair, in exciting respiratory movements, is easily shown. Thus, Pflüger† observed that, on opening the abdomen and uterus of a pregnant rabbit at the full time, the fœtuses were brought into view enveloped in the membranes, and quiescent. On detaching the placenta a few feeble inspiratory movements occurred, especially when the animals were pinched; but death soon took place. When, however, the membranes were laid open, lively inspiratory movements followed, which soon became rhythmical. In the same way it has long been a well-known fact that the first inspiratory effort of the new-born infant is most vigorously performed when the cool external air comes into contact with the face; and that impressions on the general surface, such as a slap of the hand on the nates, are often effectual in exciting the first inspiratory movements, when they would not otherwise commence. Dr. M. Hall has mentioned the important fact, that although, if the cerebrum be removed, and the pneumogastrics be divided, in a young kitten, the number of acts of respiration will be reduced to four in a minute, yet by directing a stream of air on the animal, or by irritating various parts of the general surface, we may excite twenty or thirty acts of respiration within the same space of time. He further remarks that in the very young warm-blooded animal, as in the cold-blooded animal, the phenomena of the excito-motor power are far more vividly manifested than in the older and warm-blooded. In the very young kitten, even when asphyxiated to insensibility, every touch, contact, or slight blow, every jar of the table, any sudden impression of the external air, or that of a few drops of cold water, induces at once energetic reflex movements and acts of inspiration. This may be looked upon as Nature's provision for the first establishment of the respiratory function in the new-born animal.‡—But the influence of the nerves of the general system is by no means wanting in the adult, as many familiar facts demonstrate. Thus, every one knows that the first plunge into cold water, or the first descent of the streams of the shower-bath, or even the dashing of a glass of cold water in the face, will produce inspiratory efforts;

* For a full account of the movements of respiration in the frog, with references to the observations of preceding writers, see H. N. Martin, "Journal of Physiology," vol. i. pp. 131 and 170, 1878–79, the latter paper written in conjunction with Dr. Booker.

† Pflüger's "Archiv," 1868, p. 61.

‡ Bernstein observes that prior to birth the thorax is in the extreme condition of contraction, and that the first act of inspiration is due to the elasticity of the walls of this cavity. Pflüger's "Archiv," 1878, Band xvii. p. 617.

and this fact has many important practical applications. Thus, in the treatment of Asphyxia, whether congenital or the result of narcotic poisoning, drowning, &c., the alternate application of cold and heat is found to be one of the most efficacious means of restoring the respiratory movements; and a paroxysm of hysteric laughter may be cut short by dashing a glass of cold water in the face. It seems not improbable that even the sympathetic nerve, which derives many fibres from the cerebro-spinal system, and which especially communicates with the pneumogastric nerves, may be one of the excitors to this function; and this perhaps not only through its ramifications in the lungs, which are considerable, but also by its distribution on the systemic vessels; so that it may convey to the spinal cord the impression of imperfectly arterialised blood through these, such as the pneumogastric is believed to transmit from the lungs.

279. The motor or "efferent" nerves concerned in the function of Respiration are those which Sir C. Bell grouped together in his "respiratory system." The most important of these, the Phrenics, arise from the upper part of the Spinal Cord; the Intercostals much lower down; whilst the Facial Nerve and the Spinal Accessory, to the latter of which, as will be shown hereafter (CHAP. XIII. SECT. 2), the motor powers of the Pneumogastric are chiefly due, take their origin in the Medulla Oblongata itself. M. Brown-Séquard* has paid particular attention to the feeble rhythmical movements of the Diaphragm in Rabbits, which are observed to occur after section of the phrenic nerves, and even after destruction of the entire spinal cord. He attributes them to the minute ganglia described by Rouget, which are found on the filaments of the Phrenic nerve. It is very remarkable that after such serious injury to the nervous system the two sides of the diaphragm, which are chiefly connected by tendon, should act synchronously; and also that the inspiratory movements of the Diaphragm should regularly alternate with those of the expiratory muscles, which in Rabbits are chiefly the external oblique muscles of the abdomen.

280. The actions of *sighing*, *yawning*, *sobbing*, *laughing*, *coughing*, and *sneezing* are nothing else than simple modifications of the ordinary movements of respiration, excited either by mental emotions, or by some stimulus originating in the respiratory organs themselves.—*Sighing* is nothing more than a very slow and long-drawn inspiration, in which a larger quantity of air than usual is made to enter the lungs, followed by a rapid and noisy forced expiration. This is continually taking place to a moderate degree; and we notice it particularly when the attention is released, after having been fixed upon an object which has excited it strongly, and which has prevented our feeling the insufficiency of the ordinary movements of respiration. Hence this action is only occasionally connected with mental emotion.—*Yawning* is a still deeper and longer inspiration, which is accompanied by a kind of spasmodic contraction of the depressors of the lower jaw, and also by a very great elevation of the ribs, in which the scapulæ partake. The purely involuntary character of this movement is sometimes seen, in a remarkable manner in cases of palsy; in which the patient cannot raise his shoulder by an effort of the will, but does so in the act of yawning. Nevertheless this act may be performed by the will, though not completely; and is one that is particularly excited by an involuntary tendency to imitation, as every one must have experienced who has ever been in company with a set of yawners.—*Sobbing* is the consequence of a series of short convulsive contractions of the diaphragm; and it is usually accompanied by a closure of the glottis, so that no air really enters.—

* Brown-Séquard, "Journal de la Physiologie," t. ii. p. 115.

In *Hiccup*, the same convulsive respiratory movement occurs, and the glottis closes suddenly, but later than in sobbing, in the midst of it; the sound is occasioned by the impulse of the column of air in motion against the glottis.—In *Laughing*, a precisely reverse action takes places; the muscles of expiration are in convulsive movement, more or less violent, and send out the breath in a series of jerks, the glottis being open. This sometimes goes on until the diaphragm is more arched, and the chest is more completely emptied of air, than it could be by an ordinary movement of expiration.—The act of *Crying*, though occasioned by a contrary emotion, is, so far as the respiration is concerned, very nearly the same as the last. Every one knows the effect of mixed emotions, in producing an expression of them which is "between a laugh and a cry."—The greater part of the preceding movements seem to belong as much to the *consensual* or to the *emotional*, as to the *excito-motor* group of actions; for, whilst they are sometimes the result of peculiar states of the respiratory organs, or of the bodily system in general, they may also be called forth by influences which operate directly through the senses, or which excite the emotions. Thus, whilst Sighing and Yawning often occur as simple results of deficient aëration, they may be brought on—the former by a depressed state of the feelings, the latter by the mere sight of the act in another person. Laughing is a jerking interrupted expiration, or series of expirations, during which the mouth and glottis remain open, and so the vocal chords are thrown into vibration, giving rise to the well-known sounds. There are at the same time facial expressions. The epiglottis also remains raised, and so the passage of foreign bodies into the larynx is facilitated. Sneezing may be provoked by sudden exposure of the eyes to bright light. Snoring consists in the vibration of the thoroughly-relaxed soft palate induced by the strong influx of air through the nose, or more frequently through the wide-open mouth. The actions of Laughter and Crying seem never to originate in the respiratory system; but to be always either expressions of the emotions, or simple results of sensations—as when crying arises from the sense of pain, and laughter from that of tickling. The origin of the act of Hiccup does not seem very clear; but the movement is probably of a purely reflex nature.

281. The purposes of the acts of Coughing and Sneezing are, in both instances, to expel substances from the air-passages, which are sources of irritation there; and this is accomplished in both by a violent expiratory effort, which sends forth a blast of air from the lungs.—*Coughing* occurs when the source of irritation is situated at the back of the mouth, in the glottis, trachea, or bronchial tubes. The irritation may be produced by acrid vapours, or by liquids or solids, that have found their way into these passages; or by secretions which have been poured into them in unusual quantity, as the result of disease; or by the simple entrance of air (especially if cold), when the membrane is in a peculiarly irritable state. Any of these causes may produce an impression upon the excitor fibres of the superior* and inferior† laryngeal branches of the Pneumogastrics, which, being conveyed to the Medulla Oblongata, gives rise to the transmission of a motor impulse to the several muscles, that combines them in an act of expiration. The act of coughing consists—1st, in a long inspiration, which fills the lungs; 2nd, in the closure of the glottis and of the larynx at its upper orifice by the approximation of the epiglottis to the walls of the pharynx (Ed. Smith) at the moment when expiration commences; and, 3rd, in the bursting open (as it

* See Rosenthal, "Die Athembewegungen," 1862; and Reichert's "Archiv," 1844.
† Burkart, Pflüger's "Archiv," Band i. p. 107.

were) of the glottis, by the violence of the expiratory movement; so that a sudden blast of air is forced up the air-passages, carrying before it anything that may offer an obstruction.—The difference between Coughing and *Sneezing* consists in this—that in the latter, the communication between the larynx and the mouth is partly or entirely closed by the drawing together of the sides of the velum palati over the back of the tongue; so that the blast of air is directed more or less completely through the nose, in such a way as to carry off any source of irritation that may be present there.—It is difficult to say how far these actions are independent of consciousness, or how far they may require the stimulus of sensation for their performance.

282. Various alterations are produced in the Lungs by section of the Pneumogastric nerves; the inquiry into the nature and succession of which were most carefully prosecuted by Dr. J. Reid;* who fully established that section of the Vagus on *one* side only does not necessarily, or even generally, induce disease of that lung; and hence the important inference may be drawn that the nerve does not exercise any *immediate* influence on its functions. When *both* Vagi are divided, however, the animal rarely survives long; but its death frequently results from the disorder of the digestive functions. Nevertheless, the power of digestion is sometimes restored sufficiently to re-invigorate the animals; and their lives may then be prolonged for a considerable time (§ 92). Some remarkable effects were observed by Dr. Reid in the Lungs of Mammals, after section of both pneumogastric nerves. This operation, in general, proves rapidly fatal, and, after death, the blood-vessels of the lungs are found to be intensely congested, a condition of broncho-pneumonia being established. Dr. Reid regarded the congestion of the blood-vessels as the first departure from the healthy state of the lung; and Schiff,† taking the same view, explained the congestion as a condition of neuro-paralytic hyperæmia, due to paralysis of vasomotor nerves which he supposed to run in the trunk of the pneumogastric nerves. Various observers, however,‡ pointed out that the inflammation might really arise from the entrance of particles of food or other foreign bodies into the larynx, which the animal was no longer able to prevent on account of the loss of sensibility of the parts supplied by the superior laryngeal nerve. This view is supported by the fact, when this has been prevented by keeping the animal on its back, and thus avoiding the entrance of saliva or food, no pneumonia occurred,§ whilst section of the recurrents alone, which paralysed the larynx, was followed by the pneumonia. When death does not result from pneumonia or asphyxia, due to collapse of the flaccid borders of the laryngeal opening, it seems to be the consequence, in birds, of fatty degeneration of the muscular fibres of the heart, or of some analogous change in mammals.‖

2. *Effects of Respiration on the Air.*

283. The total amount of air which can be drawn into the Lungs by the deepest possible inspiratory movement by no means affords a measure of the quantity which they ordinarily contain. It is in fact composed, as was first pointed out by Mr. Julius Jeffreys,¶ of several different quantities, which may be distinguished as follows:—

* Op. cit.

† Schiff, "Archiv f. Phys. Heilkunde," Band vi.; Falk, "Archiv f. Experim. Pathol.," Band vii. 1877, p. 183.

‡ As Traube, Friedländer and v. Boddart, "Journal de la Physiol.," vol. v. 1862, pp. 442 and 527.

§ Steiner, "Physiologie," 1878, p. 306.

‖ See Eichhorst, "Die Trophischen Beziehungen der Nervi Vagi zum Herzmuskel," Pamphlet, Berlin, 1879.

¶ "Statics of the Human Chest," 1843.

1. *Residual Air:* that which cannot be displaced by the most powerful expiration, which always remains in the thorax so long as the lungs retain their natural structure, and over which, therefore, we have no control.

2. *Supplemental Air:* that portion which remains in the chest after the ordinary gentle expiration, but which may be displaced at will.

3. *Breathing* or *Tidal Air:* that volume which is displaced by the constant gentle inspiration and expiration.

4. *Complemental Air:* the quantity which can be inhaled by the deepest possible inspiration, over and above that which is introduced in ordinary breathing.—The amount which can be expelled by the most forcible expiration after the fullest inspiration, and which is consequently the sum of the supplemental tidal and complemental air, is designated by Dr. Hutchinson* as the *Vital Capacity*, being that volume of air which can be displaced by *living movements*. This "vital capacity" is less dependent than might have been supposed upon the absolute *dimensions* of the thoracic cavity, being yet more influenced by its *mobility*. Thus, of two sets of men of the same height, one measuring 35 inches round the chest, and the other 38 inches, the average vital capacity of the first was found to be 235 inches, and that of the second only 226 inches; for, notwithstanding the greater absolute capacity indicated by the larger circumference of the latter, the inferior mobility of the chest caused more "residual air" to remain behind after the deepest expiration. By taking the average of nearly 5000 observations, Dr. Hutchinson has arrived at the very remarkable conclusion,† that of all the elements whose variation might be supposed to affect the "vital capacity," *Height* alone seems to have any constant relation to it; and that this relation is capable of being expressed in a simple numerical form. It may be briefly expressed by the rule, that *for every inch of stature, from five to six feet, eight additional cubic inches of air* (60° Fahr.) *are given out by a forced expiration after a full inspiration:* the vital capacity for a man from 5 feet to 5 feet 1 inch being 174 cubic inches; from 5 feet 1 inch to 5 feet 2 inches, 182 cubic inches, and so on.‡—There is also a relation between "vital capacity" and *Weight;* but of a different kind from that which might have been anticipated. So far as the increase in weight is simply proportional to the increase in height, the relation is, of course, the same for the one as for the other. But if the excess of weight should depend upon corpulence, the vital capacity *decreases* in a very marked manner, being always very low in corpulent men. The general result of Dr. Hutchinson's observations on this point is expressed by him as follows:—When the man exceeds the average weight (at each height) by 7 per cent., *the vital capacity decreases* 1 *cubic inch per lb. for the next* 35*lbs. above this weight.*—The influence of *Age* upon the "vital capacity" is less marked than might have been anticipated. The general fact seems to be, that the "vital capacity" undergoes a slight increase between fifteen and thirty-five years, and then gradually decreases, the decline being more rapid than the augmentation, so that by the age of sixty-six it has diminished to about 4-5ths of the maximum.—There does not seem to be as close a relation between the "vital capacity" and *Muscular Vigour* as might *à priori* have been expected, and as an attempt has been made to establish.§ Cases are not unfrequent in which men of athletic constitution have an absolute deficiency, whilst others,

* "Cyclop. of Anat. and Physiol.," vol. iv., Art. 'Thorax.' † Op. cit., p. 1072.

‡ For similar results obtained by an ingenious method suggested by M. Gréhant see "Med.-Chir. Rev.," 'Report on Physiology,' Jan. 1865, p. 231. The average vital capacity of Englishmen is given by Landois at 3772 C. cmts., and of Germans by Haeser at 3222 C. cmts.

§ See Dr. Jackson in "American Medical Examiner," 1851, p. 51.

by no means remarkable for physical power, present a large excess.* In fact, as Dr. C. R. Hall has justly remarked, this measure indicates, not what a person *does* breathe, but what he *can* breathe.—The *maximum* "vital capacity" met with by Dr. Hutchinson in his entire series of observations was 464 cub. in.; this was in a man 7 feet high, whose weight was 308 lbs. The *minimum* was no more than 46 cub. in.; this was in a dwarf (Don Francisco) whose height was only 29 inches, and weight 40 lbs. It is considered by Dr. Hutchinson† that a deficiency of 16 per cent. (unless the individual should be very corpulent) should excite suspicion of disease; but the observations of Dr. C. R. Hall (loc. sit.) seem to show that the range is considerably wider, especially in females. The vital capacity diminishes when the pressure of the air is quickly reduced, as in ascending a mountain, but after a few days' exposure to the reduced pressure the vital capacity is re-established.‡

284. In estimating, however, the effects of the Respiratory function upon the air which passes through the lungs, we are not so much concerned with the quantity which *may* be drawn in and forced out, as with that actually exchanged at each movement. The estimates of the earlier observers, Herbst, Valentin,§ &c., which ranged from 10 to 92 cub. in., are in general imperfect, having been based upon comparatively few respirations, and without taking into consideration the many circumstances we now know to exercise an influence upon the depth and frequency of the respiratory acts. Dr. Ed. Smith‖ has arranged a spirometer, by which the quantity of air inspired may be registered from 1 to 1,000,000 cub. in., and therefore for any period. He has used it for 24 hours without intermission, except for meals, and ascertained the quantity of air inspired during sleep, and in almost every condition met with during the day. From numerous experiments upon several persons, each extending over a whole day, he found that the average depth of inspiration was 33·6 cub. in. when at rest, and when walking at 1, 2, 3, and 4 miles per hour, 52, 60, 75, and 91 cub. in., and even 107 cub. in. when working the treadmill. If we take 30 or 40 cubic inches as the average quantity exchanged at each respiration, we cannot but observe how small a proportion it bears to the entire amount which the lungs usually contain; for the "residual air," which cannot be expelled, is estimated by Dr. Hutchinson at from 75 to 100 cubic inches, and the "supplemental air," which can only be expelled by a forced expiration, is about as much more; the sum of the two being from 150 to 200 cub. in., or from 5 to 7 times the "breathing volume."

* See Dr. C. Radclyffe Hall in "Trans. of Prov. Med. and Surg. Assoc.," 1851.

† Op. cit., p. 1079.

‡ See Rattray, "Proceed. Roy. Soc.," 1870, p. 513, 1872, p. 2, and F. Cresswell Hewett, "Brit. Med. Journ.," vol. ii. 1875, p. 667. In Mr. Hewett's experiments on two officers who climbed Madeira, 2950 feet, the reduction of vital capacity on the first day after the ascent was about 23 cub. inches, and the normal amount was reached in three days. He explains it by the hypothesis that the lungs become accommodated through hyperæmia to the diminished pressure, but it might also be explained by admitting fatigue of the muscles effecting forced inspiration.

§ The following are some of the amounts assigned by different observers:—

Herbst		20—30 cubic inches.
Valentin		14—92 ,,
Vierordt		10—42 ,,
Coathupe		16 ,,
Hutchinson	average	16—20 ,,
	extreme	7—77 ,,
Gréhant		0·510 of a litre.

(Gréhant, Robin's "Journal de l'Anatomie," t. i. p. 523.)

‖ Many of the following statements respecting Dr. Edward Smith's experiments were kindly communicated by himself.

Now, it is obvious that if no provision existed for mingling the air inspired with the air already occupying the lungs, the former would penetrate no further than the larger air-passages; and as this would be again thrown out at the next expiration, the bulk of the air contained in the lungs would remain altogether without renewal, and the expired air would not be found to have undergone any change.* That a change *is* effected, however, in the whole volume of the air contained in the lungs, with every inspiration, is indicated by the difference between the inspired and expired air; and its amount has been ascertained by Gréhant by means of his method, in which hydrogen gas is inspired, to be that about two-thirds of the pure air inspired remains in the lung, whilst the other third is expelled mingled with two-thirds of vitiated air.†

285. The *total amount* of air which passes through the lungs in twenty-four hours will, of course, vary with the extent and frequency of the respiratory movements; and these are liable to be affected by many circumstances, but particularly by the relative degrees of repose and of exertion. Moreover, as any such computation must be based upon the datum of the ordinary volume of breathing or "tidal" air, it is obvious that the estimates of different observers must vary with the amount they adopt. Dr. Ed. Smith found that during the day (6 A.M. to 12 night) the average quantity of air inspired by several persons at rest was 502 cub. in. per minute, or a total of 542,160 cub. in. (nearly 314 cub. feet); and as the average quantity during the night was about 400 cub. in. per minute, the total daily amount was 686,000 cub. in. (397 cub. feet), which is in close approximation to the results of Valentin, who estimated the total daily amount at 688,348 cub. in. The quantity is largely increased by exertion, and Dr. Smith computes that the total amount actually respired by the unoccupied gentleman, the ordinary tradesman, and the hard-working labourer, would be 804,780 cub. in., 1,065,840 cub. in., and 1,568,390 cub. in.; and with 12 hours of Alpine walking, as over the Wengern Alp, 1,764,000 cub. in. (1020 cub. feet). When carrying weights, as by the soldier in his heavy marching order, Dr. Smith found an increase of 7 cub. in. per minute for every 1 lb. weight carried.

286. The *alterations* in the Air‡ which are effected by Respiration, consist

* See Mr. Jeffreys' "Statics of the Human Chest," in which this important point first received due consideration.

† See for an account of his method, Budge, "Compendium de Physiologie," trad. par Eugène Vincent, 1874, p. 78.

‡ The volumetric composition of ordinary atmospheric air in England is thus given by Dr. Miller ("Elements of Chemistry," vol. ii. p. 455):—

Oxygen	20·61	Nitric Acid, Ammonia, and Carburetted Hydrogen	traces.
Nitrogen	77·95		
Carbonic Acid	0·04	And in towns—Sulphuretted Hydrogen and Sulphurous Acid.	traces.
Aqueous Vapour	1·40		

The composition by weight of pure dry air is O. 23·015, N. 76·985. When fully saturated, air at 50° F. is stated by Pettenkofer to contain about 4 grains of water per cubic foot, at 60° F. it contains about 7. The average hygrometric condition of the atmosphere at 50° F. is such that it contains about 3 grains per cubic foot, or about 75 per cent. of its full saturation. At the ordinary temperature of the month of July, the atmosphere is capable of containing nearly three times as much aqueous vapour as in December; nevertheless, the quantity of moisture actually present is generally greater in winter, owing to the greater rainfall. In air blowing over a wide expanse of sea, and after thunderstorms, a certain portion of the oxygen appears to possess the properties of ozone. Its presence is recognised by its power of decomposing potassium iodide, and causing paper dipped in a solution of this salt and starch-paste to turn blue, but no means are known of determining its quantity. Ozone disappears in air that has blown over even a narrow belt of houses, as was shown many years ago by Faraday at Brighton, and is rarely present in the air of rooms. Its action is not known, though it is generally considered to be stimulating and invigorating, and Schönbein regards it as the cause of catarrhal affections.

in its saturation with aqueous vapour, the elevation of its temperature to 97°·6 Fahr.,* and in the removal of a portion of its *oxygen*, and the substitution of a quantity of *carbonic acid* usually rather less in bulk than the oxygen which has disappeared. Very small quantities of Ammonia, of Light Carburetted Hydrogen, of Hydrogen and Nitrogen, with some volatile organic compounds which communicate an odour to the breath, are also eliminated by the lungs. Probably about 4·38 per cent. may be taken as the average amount of Carbonic acid added to the air, at the ordinary rate of respiration; whilst, according to Vierordt, the amount of oxygen removed is 4·782 per cent.; the absolute diminution in bulk of the expired air, when deprived of the moisture which it has acquired in passing through the lungs, being from 1-40th to 1-50th of its volume (1 : ·906), though its weight, owing to the sp. gr. of carbonic acid being greater than that of oxygen, is rather increased. Supposing the entire amount of air respired per diem to be 1,000,000 c. i., or 578 cubic feet, or 3600 gallons, as given by Dr. Smith for an ordinary tradesman, the absolute quantity of oxygen withdrawn from the air in the respiratory acts may be estimated at about 5000 cubic inches, or 30 c. ft. (= 5 per cent.); the weight of which would be about 18,000 grains, or rather more than $2\frac{1}{2}$ lbs. avoirdupois (Vierordt estimates it at 11,484 grains = 516,500 C. cmtr.). A curious calculation has been made by Welcker, to the effect that the surface presented for aëration, by the entire mass of the red corpuscles of the blood, amounts to no less than 2816 square metres, or estimating the amount propelled through the lung in each second to be 176 cubic centimetres, the surface presented by the corpuscles contained in that quantity of blood would amount to 87 square metres, or a square of 13 military steps to the side. It is deserving of notice in regard to the elimination of Carbonic acid, that if the air be already charged to some extent with this gas, the quantity exhaled is much diminished (Allen and Pepys).

287. The absolute quantity of Carbonic acid exhaled from the Lungs is liable to variation from so many sources that no fixed standard can be assigned for it. The mean of a great number of observations, however, made in different modes and under different circumstances, would give about 160 grains of Carbon per hour as the amount set free by a well-grown adult man, under ordinary circumstances. Taking this as the average of the twenty-four hours, the total quantity of Carbon thus daily expired from the Lungs would be 3840 grains, or 8 oz. troy, which is equal to 14,080 grains of Carbonic acid.† Vierordt gives a lower estimate—viz., 13,889 grains = 455,500 C. cmtr. at 0° C. and mean pressure. According to Dr. Edward Smith, who has devised an apparatus by which all the Carbonic acid exhaled may be collected for a whole day without intermission except for food, the total amount evolved in 24 hours at rest (deduced from experiments on different persons) was 7·144 ozs. of Carbon; and he estimates that it should be increased to 8·68 ozs. and 11·7 ozs. for the non-labouring and laborious classes respectively, at their ordinary rate of exertion. The chief causes of variation are—the Temperature and Hygrometric state of the surrounding Medium, Age, Sex, Development of the Body, Nature and Quantity of Food and state of the Digestive process, Muscular Exertion or Repose, Sleep or Watchfulness, Period of the Day, Season, and state of Health or Disease. These will now be considered in detail :—

* Weyrich, "Observations on the Insensible Perspiration of the Lungs and Skin," 1865. The temperature of the expired air varies to some extent with the temperature of the air inspired. Thus air inspired at 20° F. only rises to 85°·5, whilst air inspired at 106° is expired at 100°·5 F.

† Scharling estimated the hourly elimination of Carbonic Acid to be on the average 36 grammes, or 556 grains, and by Panum it is given as 34 grammes, or 525 grains.

I. *Temperature of surrounding Medium.*—The amount of Carbonic acid exhaled by warm-blooded animals is greatly *increased* by external *Cold*, and *diminished* by *Heat*. From Letellier's* experiments it appears that the quantity of Carbonic acid exhaled by Mammals between 86° and 106° is less than *half* that set-free near the freezing point; whilst that which is exhaled between 59° and 68° is but little more than *two-thirds* of the same amount. The diminution occasioned by heat is still more remarkable in Birds; which exhale at the highest temperature scarcely more than *one-third* of that set-free at the lowest.—The observations of Vierordt† upon himself show that the same is true of the human subject; and a difference of 10° Fahr., according to him, produces a variation of rather more than two cubic inches in the amount of Carbonic acid hourly expired. Dr. Ed. Smith found that sudden increase of temperature occasioned sudden decrease, in an increasing ratio, in the quantity of Carbonic acid evolved, amounting to 1·3 grain per minute for 16° Fahr. of temperature; but that in experiments continued over long periods there was the greatest diversity in the proportion of Carbonic acid evolved to each degree of temperature.

II. That the *Hygrometric state of the Air* influences the rate of exhalation of Carbonic acid appears from some experiments by Lehmann made with this express view. For he found that while 1000 grammes' weight of Pigeons yielded, in *dry* air, 6·055 grammes of Carbonic acid per hour, at the temperature of 75°, and 4·69 grammes at the temperature of 100°, the same animals, in *moist* air, yielded 6·769 grammes at 73°, and 7·76 grammes at 100°. And while 1000 grammes' weight of Rabbits exhaled, in *dry* air, 0·451 gramme per hour, at a temperature of 100°, they exhaled as much as 0·677 gramme in a *moist* atmosphere at the same temperature.‡

III. The amount of Carbonic acid exhaled increases in both sexes up to about the thirtieth year; it remains stationary until about the forty-fifth; and then it diminishes. Thus, according to Andral and Gavarret,§ at 8 years of age, 77 grains of carbon are excreted per hour; at 14 years, 126 grains; at 20 years, 166 grains; at 48 years, 162 grains; and at 76 years, 92·4 grains.

IV. *Sex.*—At all ages beyond eight years, the exhalation is greater in Males than in Females. Nearly the same proportionate increase takes place, however, in Females, up to the time of puberty; when the quantity abruptly ceases to increase, and remains stationary so long as they continue to menstruate. When, however, menstruation has ceased, the exhalation of Carbonic acid begins again to augment; and then again diminishes, with the advance of years, as in men. Should menstruation temporarily cease at any time, the exhalation of Carbonic acid immediately undergoes an increase, precisely as at the final cessation of the function. During pregnancy, the exhalation increases in like manner.

V. *Development of the Body.*—The more robust the individual, *cæteris paribus*, the more Carbonic acid is exhaled; and the variation is much more influenced by the development of the muscular system, than by the height or weight, capacity of the chest, &c. Thus, a very strong man of twenty-six years of age exhaled at the rate of 217·1 grains of carbon per hour; while a man of moderate muscular power set-free but 169·4 grains in the same time. Another robust man of sixty years of age exhaled at the rate of 209·4 per hour; and an old man of ninety-two years, who still preserved an uncommon degree of

* "Annales de Chimie et de Physique," 1845; and M. Boussingault's "Mémoires de Chimie Agricole et de Physiologie," 1854.

† "Physiologie des Athmens," pp. 73–82.

‡ Lehmann, Op. cit., Band iii. p. 304.

§ "Annales de Chimie et de Physique," 1843.

energy, and who in his younger days had boasted of extraordinary muscular powers, exhaled at the rate of 135·5 grains per hour. So, also, a remarkably vigorous young woman of nineteen years exhaled at the rate of 107·8 grains per hour; and a strong woman of forty-five years (who had ceased to menstruate), 152·4 grains.—On the other hand, a slender man of forty-five years, in the enjoyment of good health, only exhaled at the rate of 132·4 grains per hour (Andral and Gavarret). In Dr. Ed. Smith's experiments the quantity of *carbon* expired per diem to each 1 lb. of body-weight was 17·07 grains, 17·51, and 17·99, at 48, 39, and 33 years of age respectively.

VI. *Nature and Quantity of the Food and State of the Digestive Process.*—It is well established that the exhalation of Carbonic acid is greatly increased by eating, and that it is diminished by fasting. Thus, Prof. Scharling states the hourly exhalation to have increased in one instance from 145 to 190, after breakfast and a walk; in another from 140 to 177, after breakfast alone; and in another from 111·9 to 188·9, after dinner. Dr. Ed. Smith on several occasions fasted for more than twenty-four hours, and collected all the Carbonic acid exhaled during the whole period, or during ten minutes at each hour of the waking day. He found the total daily amount of carbon exhaled at rest and whilst fasting to be 5·923 ozs.; and there was scarcely any variation in the hourly quantity during the hours of the day. He noticed that there was a line below which the quantity of Carbonic acid did not fall, during waking hours in health; this, which he has termed the *basal line*, is that observed at rest and in the absence of food. The increase above that line, which is caused by food, seldom exceeds one-half of the basal quantity, or about 3 grains per minute. He has shown that the increase is from 2 to 3 grains per minute after breakfast and tea, and from 1 to 2 grains per minute after early dinner, whilst he scarcely found any increase after supper. He has examined the influence of numerous foods, as flesh, fish, albumen, gelatin, bread, rice, oatmeal, cane, grape, and milk sugar, milk, tea, coffee, cocoa, starch, gluten, butter, olive oil, alcohol, rum, gin, brandy, sherry and port wine, beer and spirits. All nitrogenous foods—gluten, casein, flesh, fish, albumen and gelatin—increased the evolution of Carbonic acid to the extent of $\frac{3}{4}$ to 1 grain per minute; but tea, coffee, bread, rice, oatmeal, milk, and sugar increased it from $1\frac{1}{2}$ to 3 grains per minute. Fats and starch did not increase it; alcohol, rum, and ales increased it from $\frac{1}{2}$ a grain to 2 grains per minute, whilst brandy and gin decreased it, and 3 ounces of wine exerted but little influence. The inhalation of the aroma of wines decreased it. All Dr. Smith's experiments were made in the sitting posture, at rest, before breakfast, and upon one substance alone in moderate quantity, the dose of which was repeated every ten or fifteen minutes, until the maximum influence had been obtained. With sugar, alcoholic liquids, tea, coffee, the maximum influence was observed in from twenty to thirty minutes; but with bread, oatmeal, milk, and flesh, it was commonly later, and continued from $1\frac{1}{2}$ to $2\frac{1}{2}$ hours. With sugar and tea there was frequently an increase of 1 grain per minute in less than ten minutes. The whole of the Carbonic acid exhaled during five minutes at a time for two hours was collected and weighed; the per-centage was not sought for. Dr. Smith has called attention to the separate action of the alcohol, aromas, sugars, and nitrogenous matters in each of the alcoholic compounds.*

* Similar though less extended and perfect observations have been made by Vierordt, Bidder, Schmidt, Pettenkofer and Voit, and Perrin ("Comptes Rendus," 1864, p. 257). See also Speck, "Centralblatt f. d. Med. Wiss.," 1876, p. 289, who finds that the greater the excess of C over H in the food, the larger is the quantity of CO_2 excreted, and the larger the

VII. *Muscular Exertion or Repose.*—The effect of bodily exercise, in moderation, is to produce a considerable increase in the amount of Carbonic acid exhaled, both during its continuance and for some little time subsequently to its cessation. According to the observations of Vierordt, the increase amounts to one-third of the quantity exhaled during rest, and it lasts for more than an hour afterwards; being manifested in the greater quantity of air respired, and in the larger per-centage of Carbonic acid contained in it. If the exercise be prolonged, however, so as to occasion fatigue, it is succeeded by a diminished exhalation.—Dr. Ed. Smith found that whilst walking at two and three miles per hour, the quantity of Carbonic acid evolved was 18·1 grains and 25·83 grains per minute, which are respectively 1·85 and 2·64 times more than that eliminated in the quiet sitting posture. With treadwheel labour the quantity varied from 42·9 grains to 48·66 grains. After the exertion had ceased, the increase continued for some time; and not the least exertion could be made, even when sitting, without disturbing the results.—In the experiments of Pettenkofer and Voit* the following results were obtained in the case of a healthy man, æt. 28, weighing 132 lbs., fed on ordinary diet, engaged in reading and cleaning watches, and extending over twenty-four hours:—

Period of the day.	Elimination of CO_2 through Lungs in grains.	Elimination of H_2O through Skin and Lungs in grains.	Amount of Oxygen absorbed.	Per-centage of the inspired Oxygen in the Carbonic Acid.
Day.				
6 A.M.—6 P.M. .	826·0	533·8	363·6	271·2
Night.				
6 P.M.—6 A.M. .	586·8	749·8	735·1	89·9
Total in 24 hours.	1412·8	1283·6	1098·7	361·1

A few days later the same man worked till exhausted.

Day	1371·1	169·69	456·9	337·9
Night	619·4	146·83	1022·5	68·2
Total	1990·5	316·52	1479·4	406·1

The connection between muscular exertion and the exhalation of Carbonic acid is most remarkably shown in Insects; in which animals we may witness the rapid transition between the opposite conditions of extreme muscular exertion and tranquil repose; and in which the effects of these upon the respiratory process are not masked by that exhalation of Carbonic acid which is required in warm-blooded animals simply for the maintenance of a fixed temperature. Thus, a Humble-Bee was found by Mr. Newport† to produce one-third of a cubic inch of Carbonic acid in the course of a single hour, during which its whole body was in a state of constant movement, from the excitement resulting from its capture; and yet, during the whole twenty-four hours of the succeeding day, which it passed in a state of comparative rest, the quantity of Carbonic acid generated by it was absolutely less.

VIII. *Sleep or Watchfulness.*—The amount of Carbonic acid exhaled during sleep is considerably less than that set free in the waking state. This is par-

quantity of O absorbed; whilst the larger the amount of H contained in the food, the smaller is the quantity of O absorbed, statements that generally corroborate the conclusions drawn by Dr. E. Smith.

* "Münchener Akad. Berichte," 1867, No. 10. † "Philos. Transact.," 1836.

icularly shown by the experiments of Scharling;* who confined the subjects of them in an air-tight chamber, within which they could sleep, take their meals, &c. Thus, in one case the hourly exhalation sank from 160 to 100, in another from 194·7 to 122·3, and in another from 99 to 75·1. With customary food and exercise Pettenkofer and Voit in one experiment found that of the total amount of Carbonic acid eliminated during 24 hours, 58 per cent. was given off during the twelve hours of the day, and 42 per cent. during the 12 hours of the night; whilst 33 per cent. of the oxygen was taken up by day, and 67 by night. Dr. Ed. Smith found that 4·88 and 4·99 grs. of Carbonic acid were exhaled per minute during light sleep from 1 to 3 A.M., and he estimates the quantity in profound sleep at $4\frac{1}{2}$ grs. He also observed that 5·7 grs., 5·94 grs., and 6·1 grs. per minute were evolved at 1.30, 2.30, and 6.15 A.M., whilst awake, the average amount during the waking day being 9·77 grs. per minute in the same person. The cause of this result is partly to be sought in the cessation of all muscular exertion (save that concerned in the maintenance of the respiration), and partly in the diminution in the dissipation of the heat of the body itself.

IX. *Period of the Day.*—Independently of these variations, which have their source in the condition of the individual, there is reason to believe that there is a diurnal cycle of change in the quantity of Carbonic acid exhaled; the *maximum* being (*cæteris paribus*) before and after noon, and the *minimum* before and after midnight. From the experiments of Scharling upon the Human subject, it would appear that the average proportion exhaled by day to that exhaled by night is as $1\frac{1}{4}$ to 1; and this difference does not seem to be affected by sleep or wakefulness. Dr. Ed. Smith found that the quantity of Carbonic acid varied at every moment; and that there were similar hourly variations in the quantity of Carbonic acid evolved, as in the rate of pulsations to which we have already referred. There was the least during the middle hours of the night, a slight increase with sunlight, a large increase after the meals, and a decrease before them, and a prolonged and inevitable fall after about 9 o'clock P.M. The proportion in the night of six hours to the day of 18 hours was in himself as 1 : 1·8. Most persons are conscious of a greater difficulty in bearing exposure to cold between midnight and early morning, than at any other period in the twenty-four hours.†

X. *Season.*—Dr. Edward Smith has investigated the influence of season by determining the amount evolved at rest, in the sitting posture, and before breakfast, daily throughout the year, and has found that the greatest amount occurs in April and May; that there is a decrease commencing in June, and continuing progressively through June, July, and August to September; and that in October, November, and December there is an increase. He considers that there is a maximum period (end of Winter and Spring), a minimum period (end of Summer to Autumn), an increasing period (Winter), and a decreasing period (early Summer). The extreme loss at the end of Summer was 3 grains of Carbonic acid per minute, or 33 per cent., and on the monthly average the loss was 17 or 18 per cent. He has applied this to the causation and treatment of disease, and has shown that the influence of the rotation of the seasons is a prime element in the *vis medicatrix naturæ*. Temperature and Barometric pressure to some extent, but very imperfectly, explained the results. A medium temperature was accompanied by the most

* "Ann. der Chem. und Pharm.," 1843; transl. in 'Ann. de Chim. et de Phys.,' 1843.

† Perhaps the smaller quantity of CO_2 exhaled by night than by day is due to less food being taken at this time. See the experiments of Henneberg, E. Schulze, Märker, and Busse on sheep in "Centralblatt f. d. Med. Wiss.," 1870, p. 353.

diverse quantities of Carbonic acid at the different seasons, but extremes exhibited marked influence.

XI. *Frequency of Respiration.*—Vierordt* found that, if he only respired *six* times in a minute, the quantity of Carbonic acid was 5·5 per cent. of the whole air exhaled; with *twelve* respirations, it was 4·2; with *twenty-four*, it was 3·3; with *forty-eight*, it was 3·0; and with *ninety-six*, it was 2·6 per cent. Considerable differences of opinion are held by different observers as to the influence of increased frequency of respiration on the total amount of Carbonic acid. On the whole it is probable that the mechanical variations of respiration have little or no influence on the absolute of Carbonic acid eliminated.† If the breath be held for 40 seconds (Vierordt), or 100 seconds (Stefan), the proportion of Carbonic acid may rise to upwards of 7½ per cent., and if the same air be breathed over and over again the proportion may attain 9 per. cent (Müller, Setschenow).

XII. *State of Health or Disease.*—Upon this very important cause of variation few accurate researches have yet been made. The *per-centage* of Carbonic acid in the expired air has been found to be unusually great in the Exanthemata, and in chronic Skin-diseases (Macgregor);‡ and it has been stated to be diminished in Typhus (Malcolm).§—Thus, the average proportion of health being about 4·3 per cent. (Vierordt), it has been seen at 8 per cent. in confluent Small-pox, at 5 per cent. in Measles, and at 7·2 per cent. in a severe case of Ichthyosis which terminated fatally; whilst in Typhus the per-centage has been found to range from 1·18 to 2·50. But these statements do not indicate the total quantity exhaled in each case.—The remarkable increase of the exhalation in cases of Chlorosis has been already noticed; in four cases recorded by Hannover, the hourly expiration was 123·6, 118·6, 116·9, and 106·3 grains; the absolute quantity diminishing as the respirations increased in rapidity. In chronic diseases of the respiratory organs, as might be anticipated, the amount of Carbonic acid exhaled undergoes a sensible diminution (Nysten‖ and Hannover).¶—Further researches are much needed on this subject; but, for obvious reasons, they cannot be readily made in severe forms of disease.—The greater part of the Oxygen absorbed in respiration is again eliminated in combination with Carbon as Carbonic acid. In the original experiments of Lavoisier on Guinea pigs, 81 per cent. of the Oxygen thus reappeared, the remaining 19 per cent., which disappeared, were believed by him to unite with hydrogen to form water. The results of Regnault and Reiset's experiments on various animals—mammals, birds, reptiles, insects, and annelids**—were almost precisely the same; the general average being, that for each kilogramme of weight of the animal there were absorbed per hour 3·0219 grammes of oxygen; whilst there were exhaled 3·2544 grammes of Carbonic acid; and they found that 80·5 per cent. of the Oxygen absorbed was discharged in combination with the Carbon, but considerable variations occurred connected with the nature of the food, a larger proportion of the Oxygen absorbed being combined with Carbon, when the food was rich in

* "Physiologie des Athmens," pp. 102–149. Panum (Pflüger's "Archiv," Band i.) and Berg ("Archiv f. Klin. Med.," Band vi.) arrived at the same results as Vierordt, but Lossen ("Zeitschrift f. Biologie") thinks that when the respirations are simply increased in number in a given time their greater shallowness compensates for their increased frequency, and no more CO_2 is given off.

† See for a discussion of this point Pflüger, "Pflüger's Archiv," Band xiv. 1877, p. 1; and Lossen, "Zeitschrift für Biologie," Band ii. p. 252.

‡ "Edinb. Monthly Journal," 1843. § "Report of Brit. Assoc.," 1843, p. 87.

‖ "Recherches de Physiologie et de Chimie Pathologique," 1811.

¶ "De Quantitate relativa et absoluta Acidi Carbonici ab Homine Sano et Ægroto Exhalati," 1845. ** See Longet's "Physiologie," 1861, t. i. p. 556.

Carbon,* amounting in Ruminants to about 100 per cent. Pettenkofer and Voit† also found the proportion of Oxygen eliminated in the form of Carbonic acid varied, in a large dog, from 52·4 to 148·2, according as he was kept altogether without food, or was fed upon a mixed diet of meat and sugar.

The Table (p. 372) shows a remarkable excess of the diurnal against the nocturnal elimination of Carbonic acid, especially after work, and a corresponding increase in the per-centage of the absorbed Oxygen which is thus discharged. On the other hand, the absorption of Oxygen appears to take place most energetically during the night, whilst taking the whole period of 24 hours into consideration, it appears that in both sets of experiments from 94 to 98 per cent. of the oxygen absorbed is eliminated in combination with Carbon as Carbonic acid. In other and still more recent researches, the same difference was not observed‡ between the day and night absorption of Oxygen and elimination of Carbonic acid, and no definite statement as to the exact proportion can therefore as yet be made. The elimination of Urea corresponded in its variations to that of the Carbonic acid, being 21·7 grammes by day and 15·5 grammes by night.

288. The effects of exposure to increased atmospheric pressure have been made the subject of experiment by various physiologists,§ but have been best illustrated by the observations made by Dr. Jaminet‖ on himself and on the workmen engaged in the construction of the Illinois and St. Louis Bridge over the Mississippi River. In the course of this work the men were engaged in excavations conducted at a depth of 115 feet below the level of the surface of the river, the pressure of the air then amounting to upwards of fifty pounds on the square inch of their bodies, exclusive of the ordinary atmospheric pressure of fifteen pounds on the square inch. No ill effects were observed, even when the pressure was greatest, whilst the men were working in the air-chambers; it was only on suddenly emerging that great exhaustion, pain in the epigastrium and spine, sickness, paraplegia, involving the bladder and rectum, and even death occurred. Great care was taken that on entering and leaving the air-chambers the workmen should remain for ten minutes or more in lock chambers, in which the pressure of air was gradually increased or diminished. The pulse and respiration usually rose in frequency on exposure to the augmented pressure, and free perspiration occurred; but it must be remembered that the air-chambers were small, and the temperature in them was many degrees above that of the open air. The Urine and Urea were at the same time increased. Speaking generally, there seems to be reason for believing that under the conditions to which the men were here subject, with moderate pressure (20 lbs. to the square inch), the activity of the physiological functions was augmented, though there seemed to be a reaction on return to ordinary pressure. In the cases in which death occurred, the Brain and Spinal cord were found to be highly congested, and their cavities filled with serum. M. Vivenot's experiments showed that an increase of pressure amounting

* Kowalewsky, "Arbeiten aus der Physiol. Anstalt zu Leipzig," 1867, p. 33, was only able to obtain about 50 per cent. of the oxygen absorbed in the carbonic acid exhaled, by means of his new apparatus, in rabbits fed on cabbage leaves.

† Prof. Haughton's Address "On the Relation of Food to Work," Brit. Med. Association Meeting, Aug. 1868.

‡ Op. cit., Feb. 1867.

§ Vivenot, Virchow's "Archiv," Band xxxiii.; C. W. Müller, "Zeitschrift für rat. Med.," Band xxxiii.; P. Bert, "Comptes Rendus," t. lxxiii. pp. 213 and 503; "Leçons sur la Respiration," and "Recherches experimentales sur la pression Barométrique," 1874, p. 508; Panum, Pflüger's "Archiv," Band i.; Fourdanet, "Influence de la press. de l'Air sur la Vie de l'homme," 1875.

‖ "Physical Effects of Compressed Air observed in the Construction of the Illinois and St. Louis Bridge, 1871."

to one-fifth of the normal decreased the respiration two, and the pulsations ten per minute; and it may be accepted as a general fact that in compressed air the respirations are diminished in number, but increased in depth, though the increase in depth is insufficient to compensate for their diminished frequency, so that upon the whole less air traverses the lungs. In compressed air the maximum respiratory capacity is notably augmented. The diaphragm and the base of the lung occupy a position below their usual level. Respiration is therefore performed with a permanently expanded condition of the thorax. This is no doubt one of the causes of the benefit experienced by asthmatics, and the effect continues for some time after return to air of ordinary pressure. The proportion of gases contained in the blood is only to a slight extent dependent on the pressure.* The experiments of M. P. Bert† have shown that when animals are made to respire pure oxygen gas under a pressure of five or six atmospheres (or, which is the same thing, when the pressure of the ordinary air is raised to 20 atmospheres) it acts like a poison—convulsions resembling those produced by strychnia occurring. These set in, in dogs, when the blood contains about 10 per cent. more oxygen than normal, and it is remarkable that the convulsions continue after the animal has been withdrawn from the pressure and its blood only contains the usual proportion of oxygen. With augmented barometric pressure the amount of Oxygen contained in the arterial blood of a living animal augments but with extreme slowness. The amount of Nitrogen increases more rapidly, but still far below what is required by Dalton's law, and the amount of Carbonic acid almost always diminishes. The effects of diminution of pressure in some respects resemble those of exalted pressure. Thus, Hoppe‡ observed that when rats were placed under the receiver of an air-pump and exhaustion made till the pressure was reduced to 2 inches of mercury, fainting and convulsion were usually induced, and when it was reduced to $1\frac{3}{4}$ in. (40 mm.) death occurred, apparently from the evolution of gas in the capillaries of the lungs, which impeded the passage of the blood. The singular effects observed by Glaisher§ in his lofty balloon ascents at an altitude of 7 miles—viz., loss of power in the arms and legs, failure of vision, and syncope, were probably due to the sudden and combined influence of cold, and an insufficient supply of oxygen. Less marked phenomena characterise the condition known to Alpine climbers as the Mal de montagne. They appear, however, at much lower levels than in aëronautic expeditions, on account, probably, of the muscular fatigue and want of sleep undergone. The symptoms of the affection—breathlessness, nausea or vomiting, palpitation, exhaustion, feeling of coldness, humming in the ears, and congestions of various parts, are usually experienced at a height of about 12–14,000 feet, and ascents of these altitudes should not be undertaken by those who suffer from disease of the heart, or who have a predisposition to apoplexy. The symptoms of the Mal de montagne are attributed by M. Lortet to the great consumption of heat that takes place in order to develop the amount of muscular force required. Nevertheless, both man and animals are capable of accommodating themselves to the diminished atmospheric pressure of great heights, the town of Potosi being 13,265 feet above the level of the sea, Ancomarco 15,258 feet, and Deba 15,920 feet.

289. The aëration of the blood may take place, not only by means of the Lungs, but also in some degree through the medium of the Cutaneous surface, which presents an extent of 1500 square centim. In some of the lower tribes

* Mathieu and Urbain, "Comptes Rendus," 1871, p. 216.
† "Comptes Rendus de l'Acad. des Sciences," 1872–73. ‡ Müller's "Archiv," 1857, p. 63.
§ Glaisher, Art. 'Aëronautics,' "Encyclop. Britannica," 1875, p. 167.

of animals, indeed, this is a very important part of the respiratory process; and even in certain Vertebrata the cutaneous respiration is capable of supporting life for a considerable time. This is especially the case in the Batrachia, whose skin is soft, thin, and moist; and the effect is here the greater, since, from the small proportion of the blood that has passed through the lungs, that which circulates through the system is very imperfectly arterialized. By the experiments of Bischoff it was ascertained that, even after the lungs of a Frog had been removed, a quarter of a cubic inch of Carbonic acid was exhaled from the skin in the course of eight hours. Experiments on the Human subject leave no room for doubt that a similar process is effected through the medium of his general surface, although in a very inferior degree, owing to the thickness of the epidermis, for by confining the body in a close chamber, into which the products of cutaneous respiration could freely pass, whilst the pulmonary respiration was measured by a distinct apparatus, Prof. Scharling* believed he had ascertained that the proportion of Carbonic acid given off by the Skin, the surface presented by this being estimated at 1·6 sq. metre, is from 1-40th to 1-60th of that exhaled from the Lungs during the same period of time, or from 350 to 500 grains per diem. Dr. Ed. Smith enclosed the whole of his body, except the head, in a caoutchouc bag, passed a current of air through it, and collected the Carbonic acid. The whole quantity obtained in Summer, including that found in the air of the room was 144 grains per diem, or somewhat more than 1 per cent. of the amount passing off by the Lungs. Reinhard,† estimated it at from 34 to 35 grains per diem (2·23 grammes); Röhrig‡ at 216 grains; Fubini and Ronchi§ at 105 grains; and Aubert,‖ at about 60 grains per diem, a quantity that is not equivalent to $\frac{1}{2}$ per cent. of the amount eliminated by the lungs (13-14,000 grains). Moreover, it has been observed, not unfrequently, that the livid tint of the skin which supervenes in Asphyxia, owing to the non-arterialization of the blood in the lungs, has given place after death to the fresh hue of health, owing to the reddening of the blood in the cutaneous capillaries by the action of the atmosphere upon them; and it does not seem improbable that, in cases of obstruction to the due action of the lungs, the exhalation of Carbonic acid through the skin may undergo a considerable increase; for we find a similar disposition to vicarious action in other parts of the excreting apparatus. There is also evidence that the interchange of gases between the air and the blood, through the skin, has an important share in keeping-up the temperature of the body (CHAP. XII.); and we find the temperature of the surface much elevated in many cases of pneumonia, phthisis, &c., in which the lungs seem to perform their function very insufficiently.

290. The total amount of Carbonic acid daily given-off from the Skin and Lungs may be estimated in another mode—namely, by determining the total amount of Carbon contained in the *ingesta*, and the amount excreted in other ways, making allowance for the difference in weight (if any) of the body. In this mode, Prof. Liebig came to the conclusion that the average amount of carbon exhaled by soldiers in barracks was 13·9 ozs. (Hessian) or very nearly 14 ozs. troy. From similar collective observations upon the inmates of the Bridewell at Marienschloss (a prison where labour is enforced), he calculated that each individual exhaled 10·5 ozs. of Carbon daily in the form of Carbonic acid; while in a prison at Giessen, whose inmates are deprived of all exercise,

* "Ann. der Chem. und Pharm.," 1846. † "Zeitschrift für Biologie," Band v. 1869, p. 37.
‡ Pflüger's "Archiv," Band vi. 1872, p. 539. § "Deutsche Klinik," 1872, p. 209.
‖ Pflüger's "Archiv," Band vi. 1872, p. 539.

the daily average was but 8·5 ozs.* A very exact estimate, though based on more limited data, was made by M. Barral,† who experimented upon himself (æt. 29) in winter (A) and in summer (B), upon a boy 6 years old (C), upon a man 59 years old (D), and upon an unmarried woman of 32 years (E). The following Table gives the results which he obtained, from an average of five days, in regard to the disposal of the Carbon of the food; those which relate to its Nitrogen, Hydrogen, and Oxygen will be noticed subsequently.

	Weight of Body.	*Carbon of Food.*	*Carbon excreted.*		
			In Fæces.	In Urine.	By Exhalation.
A	104·5 lbs.	5654·1 grs.	236·2 grs.	234·6 grs.	5183·3 grs.
B	——	4090·0 „	137·4 „	211·5 „	3741·1 „
C	33 „	2382·3 „	149·7 „	67·9 „	2164·7 „
D	129·1 „	5123·0 „	210·0 „	327·3 „	4585·7 „
E	134·6 „	4520·8 „	64·8 „	216·1 „	4239·9 „

Thus, the average amount of the Carbon daily consumed in pulmonary and cutaneous exhalation by M. Barral himself, was in winter 5183·3 grains, or 10·8 ozs. troy; whilst in summer it was but 3741·1 grains, 7·8 ozs. troy. This difference is quite conformable to what might have been anticipated from the results of a different mode of experimenting; and it throws some light on the discrepancies in the results of other measurements, to find that the seasonal variation is scarcely less than one-third of the mean between these two amounts. The other results correspond closely with the statements of MM. Andral and Gavarret, in regard to the higher proportion of Carbonic acid exhaled (as compared with the bulk of the body) by children, and the smaller proportion thrown off by men advanced in years, and by women. In some experiments made on himself in Pettenkofer's apparatus, Ranke (weighing 161 lbs.) found that, when at rest and fasting, 10,190 grains of Carbonic acid or 2779 grains of Carbon were eliminated in twenty-four hours by the Skin and Lungs, whilst with as full a diet as possible the amount was 13,278 grains of Carbonic acid or 3621 grains of Carbon. Rubini and Ronchi experimented on the fore-arm and hand confined in a chest, and found that more CO_2 gas is given off by day than by night in the proportion of 113 : 100. The quantity rises, with augmented temperature, considerably. It is during fasting (15–18 hours after the last meal) somewhat less than during digestion, the proportion being as 100 : 112. It is greater with pure vegetable than with animal food. The amount in one individual eliminated in 24 hours was 425 millegrammes. A certain interchange of gases must also take place in the intestinal canal. This, though of small amount in man, is of considerable importance in many of the lower animals, as in many fish and insects.

291. It is not only by an oxygenated atmosphere that the removal of Carbonic acid from the blood may be effected. For although it was formerly supposed that the exhaled Carbonic acid is generated in the lungs by the combination of atmospheric oxygen with the carbonaceous matters of the blood, and that the inhalation of oxygen is therefore immediately necessary for its production, yet it is now quite certain that this Carbonic acid exists preformed in venous blood, and that the oxygen introduced is carried into the arterial circulation, instead of being at once returned to the air in a state of Carbonic acid. Hence an exhalation of Carbonic acid may continue for a considerable period (in cold-blooded animals especially), whilst the animal is breathing an atmosphere in which no oxygen exists. Thus, it was shown by Spallanzani,‡ that snails might be kept for a long time in Hydrogen without

* Op. cit., p. 46. † "Ann. de Chim. et de Phys.," tom. xxv.
‡ "Mémoires sur la Respiration," traduit par Senebier, Genève, 1804.

apparent injury to them; and that during this period they disengaged a considerable amount of Carbonic acid. Dr. Edwards* subsequently ascertained that, when Frogs were kept in hydrogen for several hours, the quantity of Carbonic acid exhaled was fully as great as it would have been in atmospheric air, or even greater. This latter fact, which, however, is very doubtful, might be accounted for by the superior displacing power which (on the laws of the diffusion of gases) hydrogen possesses for Carbonic acid. Collard de Martigny† repeated this experiment in Nitrogen, with the same results. In both sets of experiments, the precaution was used of compressing the flanks of the animal, previously to immersing it in the gas, so as to expel from the lungs whatever mixture of oxygen they might contain. These experiments have since been repeated by Müller and Bergmann, who took the additional precaution of removing, by means of the air-pump, all the atmospheric air that the lungs of the frog might previously contain, together with the Carbonic acid that might exist in the alimentary canal. They found, in one of their experiments, that the quantity of Carbonic acid exhaled in hydrogen was nearly a cubic inch in $6\frac{1}{2}$ hours; and in another, that nearly the same amount was given-off in nitrogen, though this required rather a longer period. It appears from the table of their results,‡ that the amount was not ordinarily greater in the experiments which were prolonged for twelve or fourteen hours than in those which were terminated in half the time; hence it may be inferred that the quantity which the blood is itself capable of disengaging is limited, and that the antecedent absorption of oxygen and its storage in the tissues§ is necessary to enable Carbonic acid to be continuously set-free from the body.—It is impossible, however, for an *adult* Bird or Mammal to sustain life for any considerable time in an atmosphere deprived of oxygen; since the greatly-increased rapidity and energy of all their vital operations necessitate a much more constant supply of this vivifying agent than is needed by the inferior tribes; and, as we shall presently see, the capillary action requisite for the passage of the blood through the lungs will not take place without it. But Dr. Edwards has shown that *young* Mammalia can sustain life in an atmosphere of hydrogen or nitrogen for a sufficient length of time to exhale a sensible amount of Carbonic acid; so that the character of the process is clearly proved to be the same in warm-blooded animals as in Reptiles and Invertebrata.

292. The seat of those changes which result in the formation of Carbonic acid has been the subject of much research and discussion. It may either be conceived that the oxygen taken up by the blood corpuscles, and feebly held in combination by their hæmoglobin, escapes by diffusion through the blood-vessels, and directly enters into combination with the constituents of the tissues, the Carbonic acid formed being given up in exchange for fresh oxygen, which is at once stored up in the tissues; or we may suppose that the products of the disintegration of the tissues enter the blood, and there meeting with the loosely combined oxygen, abstract it from the corpuscles, which readily surrender it to the more oxidizable materials. In the one case, the oxidizing process and the production of Carbonic acid would take place chiefly in the tissues, in the other chiefly in the blood. Various circumstances seem to point to the former as being the more correct statement of the facts.‖ In the first place, the respiration of the tissues shown to occur by Liebig and P. Bert

* "De l'Influence des Agens Physiques sur la Vie," Paris, 1824.

† 'Recherches Expérimentales,' &c. in Magendie's "Journal de Physiologie," tom. x.

‡ Müller's "Elements of Physiology," translated by Baly, vol. i. p. 338.

§ Pflüger, Pflüger's "Archiv," Band x. p. 251, 1875.

‖ See J. Worm Müller, in Ludwig's "Arbeiten," 1870, p. 168. 'Ueber die Spannung des Sauerstoffs der Blutscheiben.'

leads to the development of Carbonic acid within them, and as they contain (at least in the case of the most important of all—the muscles) no oxygen capable of being removed by exhaustion, the oxygen contained in arterial blood will in obedience to physical laws diffuse into the tissues, and be replaced by Carbonic acid. Again, it may be shown that arterial blood loses its oxygen with extraordinary rapidity during its passage through the capillaries, and although this was attributed by Schmidt to the presence of easily oxidizable or reducing substances in the blood, chiefly associated with the corpuscles (Afanassieff), yet Pflüger* has shown that the quantity of these oxidizable substances can be but small, since arterial blood removed from the body only slowly acquires a venous character, whilst even in the case of asphyxiated animals, warmth and time are required for the production of a large amount of Carbonic acid; and so too, if an easily oxidizable substance, as sodium lactate, glycerin, grape sugar, or caproic acid, be added to blood after withdrawal from the body, no augmentation in the amount of Carbonic acid is observed, though if injected into the circulation such substances are quickly decomposed, and cause increased evolution of this gas.† The fact noticed by Ludwig and Hammarsten, that the tension of the Carbonic acid in the lymph is lower than in venous blood, though higher than in arterial, constitutes no valid objection to the view that the gas is chiefly formed in the tissues and not in the blood, since the lymph examined by them had already had the opportunity of equalizing the tension of its gases with those of arterial blood in traversing the lymphatic glands and the lacunæ of the connective tissues. At the same time, the phenomena of oxidation are materially affected by the integrity of the blood corpuscles, since these are the carriers of the oxygen, or perhaps, more properly speaking, of ozone; for, as Ritter‡ has shown in his investigations on the influence of agents which modify the absorptive capacity of the corpuscles for oxygen, the secretions undergo material alterations when the corpuscles have been profoundly altered by the action of antimonial and arsenical compounds, by phosphorus, or by the action of the biliary acids; these agents changing the form of the corpuscles, and causing the appearance of crystals of Hæmoglobin in the blood, coinciding with which the urine becomes albuminous, and contains various colouring materials. In connection with this, the observations of Manassein§ may be mentioned, as showing that the red corpuscles diminish in volume when under the influence of abnormal activity of the disintegrating processes, as in Febrile states when they have to part with an increased amount of oxygen; or when any obstacle exists to the absorption of oxygen, as when they are exposed to the action of carbonic acid or morphia; whilst they augment in size when they are exposed to a highly oxidized medium, or when they are placed under conditions in which the oxygen escapes with difficulty, as after the administration of refrigerants, quinine, alcohol, and hydrocyanic acid. Whether the carbonic acid is chiefly formed without or within the vessels, it is certain that the amount developed

* Pflüger, 'Ueber die Diffusion des Sauerstoffs, &c.,' Pflüger's "Archiv," Band vi. 1872, p. 43.

† Ludwig and Schremetjewsky (Ludwig's "Arbeiten," 1868) have, however, shown that sugar passes through the capillaries of the kidneys unchanged. It has been shown by Oertemann (Pflüger's "Archiv," Band xv. 1877, p. 381) that if a frog be thoroughly deprived of blood, and the vessels refilled with ·75 per cent. solution of common salt, life may be preserved from two to three days.

‡ Ritter, "Des Modifications chimiques que subissent les secretions sous l'influence de quelques agents qui modifient les globules sanguins." Paris, 1872. See Kuss, "Physiologie," p. 380.

§ "Ueber die Dimensionen der rothen Blutkörperchen unter verschiedenen Einflüssen." Pamphlet, 1872.

bears a close relation in all parts of the body with the energy with which cell growth and function take place, and with the activity of the interstitial changes coincident with these processes; the blood, which has then become charged with this gas and poor in oxygen, is conducted to the lungs, when the converse changes are effected, the Carbonic acid diffusing through the vessel into the air contained in the pulmonary alveoli, and being replaced by oxygen. On the whole, the absorption of oxygen from the air into the venous blood is to be regarded as an exclusively chemical process, and as dependent upon the affinity of reduced Hæmoglobin for Oxygen, for the quantity of oxygen absorbed is the same whether the animal breathe pure oxygen or a mixture of oxygen and nitrogen, and an animal placed in a confined space continues to breathe till nearly all the oxygen is used up. The tension of the oxygen in the blood is very low, amounting in arterial blood to 29·6 mm. of mercury, which corresponds to an amount of 3·9 per cent., and in venous blood to 22 mm., corresponding to 2·9 per cent.,* whilst the tension of the O of the atmospheric air amounts to 158 mm. of mercury, corresponding to the presence of 20·8 vol. per cent. The elimination of Carbonic acid, on the other hand, from the blood is partly due to its expulsion by the oxygen which takes its place, and partly to the high tension at which it exists, and the natural tendency to diffusion. The tension of the Carbonic acid gas in arterial blood is equal to 21 mm. of mercury, corresponding to 2·8 vol. per cent., and in venous blood to 41 mm., corresponding to 5·4 vol. per cent., whilst the tension of this gas in the air is only 0·38 mm., corresponding to 0·03–0·05 per cent; there is consequently a strong tendency for the Carbonic acid to escape from the blood and to diffuse into the air contained in the alveoli of the lungs. This is regarded as the effect of the formation of oxyhæmoglobin, the expulsion of the Carbonic acid being dependent on the absorption of oxygen.

293. Much discussion has taken place with regard to the degree in which the proportion of *Nitrogen* in the air is affected by Respiration. It seems probable that the absorption and exhalation of this gas are continually taking place; but that the two amounts usually nearly balance each other.† On the whole, however, there is adequate reason to believe that Nitrogen is ordinarily given-off; this being the joint result of the analysis of the expired air, and of the comparison of the amount of nitrogen given-off in the other excretions with that ingested as a constituent of the food. In some experiments made by Regnault and Reiset, on the composition of the expired air in various warm-blooded animals, they arrived at the following conclusions:—(1). That warm-blooded animals subjected to their ordinary regimen exhale nitrogen, but never in larger proportion than 1–50th, and sometimes in less than 1–100th, of the oxygen consumed;—(2). That in a state of inanition, animals usually absorb nitrogen;—(3). That animals whose usual diet has been changed, usually absorb nitrogen until they are accustomed to their new food.‡—Voit,§ in experiments on pigeons extending over 124 days, found that little or no nitrogen is eliminated by the lungs in these animals, since the amount contained in the urine and fæces was equal to within 2·3 per cent. of that ingested. This result is in marked contrast to that obtained by Boussingault, who found a deficit of 35 per cent. of nitrogen in the fæces and urine, when compared with that contained in the food. From Seegen's researches

* Worm Müller, Ludwig's "Arbeiten," 1871, p. 119.

† For the considerations which render this probable, see especially Dr. W. F. Edwards, "On the Influence of Physical Agents on Life," part iv. chap. xvi. sect. 2, 3.

‡ "Ann. de Chim. et de Phys.," 1849; and "Mém. de Chim. Agric.," 1854, p. 31.

§ Henle and Meissner's "Bericht," 1862, p. 342, and 1866, p. 390.

on dogs,* it appears that although generally the greater part of the nitrogen is eliminated as urea, under certain circumstances a large portion (one half) may be discharged by other channels, a portion probably escaping by the lungs; and more recently Seegen, in conjunction with Nowak† have satisfied themselves that nitrogen is eliminated in the proportion of 5·7 to 6·0 ingested in the gaseous form or about 10 per cent. of the total excretions of nitrogen. Barral estimated that the amount of nitrogen which (being otherwise unaccounted for) must be considered to have passed off by the lungs and skin in Man, varied from 1-75th (in an adult) to 1-143rd (in a child) of the nitrogen consumed, the former proportion agreeing very well with that deduced by MM. Regnault and Reiset from their experiments on animals.

[The alterations effected in the *Blood* by Respiration have already been fully considered. See §§ 196-197.]

294. *Exhalation and Absorption through the Lungs.*—The Air expired from the lungs differs from that which was introduced into them, not merely in the altered proportions of its Oxygen, Nitrogen, and Carbonic acid, but also in having received (under ordinary circumstances, at least) a large addition to its watery vapour. This it doubtless acquires in accordance with physical laws, through its exposure to the warm blood which is spread-out over a very extensive surface, the intermediate membrane being extremely permeable; and the variations in its amount will depend upon the physical conditions under which that exposure takes place. The air expired in ordinary respiration is charged with as much watery vapour as saturates it at the temperature of the body;‡ and consequently the amount of watery vapour thus exhaled will vary (for equal volumes of air at any given temperature) in the inverse proportion to that which the air previously contained. But when the air is very cold and very dry, and the respiration is unusually rapid, or when the amount of fluid in the body is greatly diminished, as after long fasting, it may not remain sufficiently long in the air-cells to be raised to the temperature of the body, or to be fully saturated with moisture. The amount of watery vapour exhaled, moreover, will of course depend in part upon the quantity of air which passes through the lungs. And from these causes of difference it happens that the amount of watery vapour exhaled in twenty-four hours may vary from about 6 ozs. to 27 ozs.; its usual range, however, being between 7 and 11 ozs.§ Weyrich‖ estimates the amount of insensible perspiration by the skin and lungs for a man weighing 125 lbs. at 14,500 grains, or 2 lbs. avoirdupois per diem, and the proportion of water discharged by the skin to that by the lungs as 2 : 3. Dr. Ed. Smith found that during a long fast the quantity of vapour exhaled by the lungs was 2·02 grs. per minute, or ·548 gr. in every 100 cub. in. of expired air. With food and at rest, the quantity varied from 3 grs. to 3·4 grs. per minute. The inhalation of alcoholic vapours increased the quantity of vapour exhaled; when alcohol was drunk the quantity was also increased, but it was decreased under the action of gin.—Of the fluid ordinarily exhaled with the breath, a part doubtless proceeds from the moist lining of the nostrils, fauces, &c.; but it is indisputable that the greater proportion of it comes from the lungs, since, when the respiration is entirely performed through a canula introduced into the trachea, the amount of watery vapour which the breath

* "Wiener Sitzungsberichte," 1867, March, Band lv.

† Pflüger's "Archiv," vol. xix. 1879, p. 347.

‡ The tension of the watery vapour of expired air amounts, according to Weyrich, when reduced, to 0° C. and 760 mm. pressure to 4·36 mm. of mercury, which is nearly that of air saturated with aqueous vapour (4·5 mm.).

§ Valentin's estimate is 8333 grains in the 24 hours from the lungs alone. Vierordt's 5092 grains.

‖ "Observations," &c., Dorpat, 1865, 8vo.

contains is still very considerable. Of the proper pulmonary exhalation, there can be no doubt that the greater part is the mere surplus-water of the blood, and especially of the crude fluid which has been newly introduced into the circulating current by the process of nutritive absorption. But there is strong evidence that Hydrogen as well as Carbon undergoes combustion in the system, and that a portion of the exhaled aqueous vapour is the product of that combustion. For of the hydrogen which the food contains, not more than from 1-8th to 1-10th passes off by the other excretions, the remaining 7-8ths or 9-10ths being exhaled in the condition of watery vapour from the lungs. A portion of the oxygen which this vapour contains is supplied by the food; but there is usually a considerable surplus of hydrogen, and this can only be converted into water at the expense of oxygen derived from the atmosphere.

295. The fluid thrown-off from the lungs is not pure water. It holds in solution, as might have been expected, a considerable amount of Carbonic acid, and also some animal matter, which, from the inquiries of Dr. R. A. Smith,* would appear to be an albuminous substance in a state of decomposition. A small quantity of Ammonia is usually, but perhaps not always, thrown-off.† It has been suggested that this, when present, may be derived either from decomposing fragments of food or from carious teeth; but Thiry believed he had demonstrated it in air expired to avoid contamination through a canula introduced into the trachea of a rabbit. The test used was Nessler's (solution of iodide of mercury and iodide of potassium). Ransome estimates that an amount of Ammonia representing about 3 grains of organic matter are eliminated by an adult man in twenty-four hours. Lossen, however, estimates it at only 0·014 grain per twenty-four hours.‡ According to Wiederhold,§ the Chlorides of Sodium and Ammonium, Uric Acid and the Urates of Soda and Ammonia, may be detected in the expired air. Ransome found a small quantity of Urea in one or two instances. If the fluid be kept in a closed vessel, and be exposed to an elevated temperature, a very evident putrid odour is exhaled by it. Every one knows that the breath itself has, occasionally in some persons, and constantly in others, a fœtid taint; when this does not proceed from carious teeth, ulcerations in the air-passages, disease in the lungs, or other similar causes, it must result from the excretion of the odorous matter, in combination with watery vapour, from the pulmonary surface. That this is the true account of it seems evident from the analogous phenomenon of the excretion of turpentine, camphor, alcohol, and other odorous substances which have been introduced into the venous system, either by natural absorption, or by direct injection; and also from the suddenness with which it often manifests itself, when the digestive apparatus is slightly disordered, apparently in consequence of the entrance of some mal-assimilated matter into the blood. Among the substances occasionally thrown-off by the lungs, Phosphorus deserves a special mention, on account of the peculiarity of the form under which it is eliminated; for it has been found that if phosphorus be mixed with oil, and be injected into the

* "Philosophical Magazine," vol. xxx. p. 478.

† See Richardson, "The Cause of the Coagulation of the Blood," 1857, p. 360; Lossen, "Zeits. f. Biologie," Band i. p. 107; Thiry, "Zeits. f. rat. Med.," Band xvii. 1863, p. 166; Schenk, Pflüger's "Archiv," Band iii.; Kühne and Strauch, "Centralblatt," 1862, p. 578; Arthur Ransome, "Journal of Anatomy and Physiology," 1870, vol. iv. p. 209; Truchot, "Comptes Rendus," 1873, t. ii. p. 1160. Bachl, however ("Zeits. f. Biologie," Band v. p. 61), was unable to find any traces of it.

‡ Foster, "Physiol.," 3rd edit., p. 266.

§ "Deutsche Klinik," 1858. Schenk states that a small quantity of ammonia is eliminated by the lungs in the Rabbit, Guinea Pig, and Dog, but none by the skin. The nature of the food has no influence on the quantity (Pflüger's "Archiv," Band iii. p. 470.

blood-vessels, it partly escapes in an unoxidized state from the lungs, rendering the breath luminous.* And this luminous breath has also been observed in spirit-drinkers, in whom the oxidation of the effete matters of the system is impeded, in consequence of the demand set-up by the alcohol ingested for the oxygen introduced (§ 290, vi). The poisonous effects of air which has been already breathed are much more marked than air charged with the same amount of Carbonic acid gas, evidently in consequence of the organic impurities with which it is charged.

296. Not only exhalation, but also (under peculiar circumstances) *absorption* of fluid may take place through the Lungs. Thus Dr. Madden† has shown that, if the vapour of hot water be inhaled for some time together, the total loss by exhalation is so much less than usual, as to indicate that the cutaneous transpiration is partly counterbalanced by pulmonary absorption; the pulmonary exhalation being at the same time entirely checked. It is probable that, if the quantity of fluid in the blood had been previously diminished by excessive sweating, or by other copious fluid secretions, the pulmonary absorption would have been much greater. Still, in the cases formerly mentioned (§ 147), in which a large increase in weight could only be accounted-for on the supposition of absorption of water from the atmosphere, it seems probable that the cutaneous surface was chiefly concerned; for it can only be when the air introduced into the lungs is *saturated* with watery vapour that the usual exhalation will be checked, or that any absorption can take place.

297. That absorption of other volatile matters diffused through the air, however, is continually taking place by the Lungs, is easily demonstrated. A familiar example is the effect of the inhalation of the vapour of Turpentine upon the urinary excretion. It can only be in this manner that those gases act upon the system, which have a noxious or poisonous effect when mingled in small quantities in the atmosphere; and it is most astonishing to witness the extraordinary increase in potency which many substances exhibit, when they are brought into relation with the blood in the gaseous form. The most remarkable example of this kind is afforded by Arseniuretted Hydrogen, the inspiration of a few hundredths of a grain of which has been productive of fatal consequences, the resulting symptoms being those of arsenical poisoning. Next to this, perhaps, in deleterious activity, is Sulphuretted Hydrogen; but it would seem that the effects of this gas upon the Human subject are scarcely so violent as they are upon animals; for though it has been found that the presence of 1-500th part of it in the respired air will destroy a bird in a very short time, that 1-800th part suffices to kill a dog, and that 1-250th part is fatal to a horse, yet M. Parent-Duchâtelet has affirmed that workmen habitually breathe with impunity an atmosphere containing *one per cent.*, and that he himself has respired, without serious symptoms ensuing, air which contained *three per cent.* There can be no doubt, however, that the *continued* inhalation of air thus contaminated would be speedily fatal. Sulphuretted hydrogen and Ammonium Sulphide are given off from most forms of decaying animal and vegetable matter; and it is undoubtedly to the accumulation of these gases that the fatal results which sometimes ensue from entering sewers are to be chiefly attributed.—Antimoniuretted and Phosphuretted hydrogen may also be included with the above as poisonous gases. These all oxidize themselves at the expense of the oxygen of the blood,‡ and as a result of this

* Casper's "Wochenschrift," 1849, Band xv.

† "Prize Essay on Cutaneous Absorption," p. 55.

‡ See the experiments of Kaufmann and Rosenthal on the action of Sulphuretted Hydrogen, in Reichert's "Archiv," 1865, Heft vi.; those of Hoppe-Seyler on the same, and on

appropriation, induce dyspnœa, convulsions, and asphyxia. Other poisonous gases, as Carbonic oxide* (practically destroying the red blood-corpuscles), Deutoxide of Nitrogen, and Cyanuretted Hydrogen, according to Hermann,† form a group that displace the oxygen and enter into combination with the hæmoglobin, producing a clear red solution, and inducing the same symptoms as the former. Deutoxide of Nitrogen is, however, properly included under the irrespirable gases. Other poisonous gases, again, as Protoxide of Nitrogen, Olefiant gas, Chloroform, and Carbonic acid, are intoxicating in their properties, affecting the functions of the brain, and ultimately producing a narcotic effect. Amongst the irrespirable gases which, unless exceedingly diluted, induce spasm of the glottis, may be enumerated Carbonic acid, Hydrochloric acid, Binoxide and Peroxide of Nitrogen, Ammonia, Chlorine, and Ozone. If introduced through a tracheal fistula, all of them act as poisons. Finally, Nitrogen, Hydrogen, and perhaps Carburetted hydrogen, may be considered as indifferent gases, proving fatal when breathed in a state of purity, by permitting the accumulation of carbonic acid in the blood, and by failing to supply oxygen.—Cyanogen is another gas which has an actively-poisonous influence upon animals, when absorbed into the lungs. Its agency is of a narcotic character, but has not been accurately investigated.

298. The respiration of pure Oxygen for short periods, 7—17 minutes in Man,‡ produces no effect either on the rapidity of the pulse or upon the temperature of the body, and scarcely any more of this gas is absorbed than under ordinary circumstances, which, as Pflüger, has shown, is owing to the fact that arterial blood is charged normally with nine-tenths of the whole amount of oxygen it can take up. In small chambers§ the whole of the oxygen is used up, but if the chamber be large, the amount of carbonic acid produced proves fatal before the complete consumption of the oxygen. If an animal be placed in an atmosphere of pure oxygen with no provision for the removal of the carbonic acid eliminated, death takes place when the proportion of this gas amounts to 20—30 per cent., though the quantity of Oxygen may still amount to from 70—80 per cent. When all the Carbonic acid eliminated is removed, as fast as formed, death occurs in mammals when the amount of Oxygen falls to 2 per cent., and in birds when it is reduced to between 3 and 4 per cent.‖ Animals made to breathe Oxygen at a pressure of 5 or 6 atmospheres, or which are exposed to ordinary air at a pressure of 20 atmospheres, fall into violent convulsions, which last even after the pressure has been reduced to the normal. It would therefore appear that the Oxygen in entering the blood at this high pressure forms one or more compounds with some of its constituents, acting like strychnia. The most interesting recent researches in regard to the effects of respiring air more or less contaminated with Carbonic acid gas, and with varying amounts of Oxygen, are those of Friedländer and Herter,¶ which, whilst generally corroborating the results obtained by M. Bert, show that a marked distinction must be drawn between

Antimoniuretted and Arseniuretted Hydrogen, "Med. Chem. Unters.," Heft i. p. 133, and those of Dybkowsky on Phosphuretted Hydrogen; Henderson, Humphrey's "Journal of Anat. and Phys.," vol. xiii. p. 109.

* See Traube, Gurlt's "Verhand. d. Berlin. Gesellsch.," 1866, p. 67, and C. Bernard, "Rev. Scientif." t. vi. 1870; and "Leçons sur les Anæsthésiques."

† "Physiologie," 1874, pp. 45 and 161.

‡ Naoumoff and Béliaieff, Robin's "Journal de l'Anatomie," 1875, p. 138. See also Kowalewsky, in "Travaux du laboratoire physiologique de l'Univ. Imp. à Kasan," 1ere sér. Kasan, 1869.

§ See account of Müller's Experiments in Funke's "Physiology," 1870, p. 284.

‖ Paul Bert, Art. 'Asphyxia,' "Nouv. Dict. de Méd.," t. iii.

¶ "Zeits. f. physiolog. Chemie," 1878, p. 99.

the effects produced by large and small quantities of Carbonic acid gas; small doses including all quantities up to 20 per cent.; large doses, quantities varying from 20 to 65 per cent. The addition of Carbonic acid gas was made solely at the expense of the Nitrogen of the air, and the amount of Oxygen in the gas mixture supplied to the animal was maintained at the normal standard of 21 per cent. With small doses, corresponding to 11—13 per cent. of Carbonic acid gas, the animals exhibited some dyspnœa, the respirations being deeper and more frequent, the action of the heart was increased, but the temperature remained unchanged, and no poisonous effects were observed, even in the course of an hour. The dyspnœa rapidly vanished when the animals (rabbits) were removed from the bell-glass under which they had been confined. When the quantity of Carbonic acid gas in the air supplied was increased to about 30 per cent. the phenomena of stimulation, above noted, lasted only for a short time, and were succeeded by depression; the respirations became feebler and shallower, the blood-pressure sank gradually, and voluntary and reflex activity gradually failed. The temperature also fell considerably, and the animal after the lapse of some hours died. With maximum doses the period of excitation became reduced in duration to a few minutes, the cardiac excitation, as indicated by the increased blood-pressure, lasting longer than the respiratory excitation, whilst the phenomena of depression soon set in, and death occurred in the course of half an hour, being preceded by arrest of the respiration and of the heart's action. In regard to the effects of a deficiency of Oxygen, it appears* that animals breathe tranquilly when the proportion of Oxygen is only 14·8 per cent.; with 7 per cent. they begin to be dyspnœic. With 4·5 per cent. the dyspnœa is severe, and with 3 per cent. there is rapid asphyxia. If the withdrawal of the supply of Oxygen be sudden, the animal being placed in an indifferent gas, dyspnœa, rapidly increasing in intensity, supervenes, with clonic spasms of the muscles of the body generally. There is then a long respiratory pause, which is followed by exophthalmus and dilatation of the pupils. Finally, a few weak respiratory movements are made before death, which usually takes place in rabbits in the course of from $1\frac{1}{2}$ to 2 minutes. Now, in the case of Carbonic acid poisoning, even when the proportion of CO_2 is 80 per cent. to 20 per cent. of Oxygen, the duration of life is at least ten times longer, and the dyspnœa is less immediate in its appearance. Loss of consciousness and of the reflex movements is observed in the course of the first minute in CO_2 poisoning, but when these phenomena occur in acute withdrawal of Oxygen it is the immediate presage of death. Moreover, CO_2 narcosis may last for half an hour without danger to life, whilst loss of consciousness from withdrawal of Oxygen can only last a very short time if life is to be preserved by admitting a fresh supply. If an animal be placed in a confined space, with a supply of ordinary air, and the CO_2 be absorbed as fast as it is formed, so as to avoid any ill effects from its accumulation, it is found that the quantity of Oxygen is reduced when death occurs from 3·8 to 2·1 per cent.† Here also dyspnœa (deeper and more frequent respiratory acts) occurred, which gradually increased to orthopnœa, the head being thrown back and the nostrils powerfully dilated. One of the most marked differences between the toxic influence of an excess of CO_2 and the withdrawal of O occurs during the last few minutes of life, which in the former is accompanied by a gradual cessation of the respiratory movements, whilst in the latter there are phenomena of violent excitation of the nervous and muscular systems which last for a few moments, and the

* W. Müller, Friedländer, and Herter, "Zeits. f. physiol. Chemie," Band iii. 1879, p. 21.

† Friedländer and Herter, loc. cit., p. 24. Bernard found it vary from 3 5 per cent.; Stroganow, Pflüger's "Archiv," Band xii. 1875, p. 30, from 3 to 4 per cent.

respiration then suddenly ceases and the animal falls dead. Post-mortem examination showed that the lungs were somewhat hyperæmic, but they rarely exhibited ecchymoses or any œdema, which is so common in CO_2 poisoning. In regard to the blood-pressure there was no primary fall as in CO_2 poisoning, but an increase which lasted till just before death, when it suddenly fell.* The pulse always fell in frequency when the quantity of Oxygen was below 4 per cent. It cannot be doubted that Miasmata and other morbific agents diffused through the atmosphere are more readily introduced into the system through the pulmonary surface than by any other; and our aim should therefore be directed to the discovery of some counteracting agents which can be introduced in the same manner. The pulmonary surface affords a most advantageous channel for the introduction of certain medicines that can be raised in vapour, when it is desired to affect the system with them speedily and powerfully; such is pre-eminently the case with the various anæsthetic agents, such as ether and chloroform, whose introduction into the various departments of Medical and Surgical practice constitutes a most important era in the history of the healing art; also with Mercury,† Iodine, Tobacco, Stramonium, &c., and it has recently been shown by M. Jousset that direct injection through the trachea is a means by which quinine may be made to enter the system rapidly, when the state of the cutaneous circulation and the irritability of the stomach render it useless to administer it either by the stomach or by subcutaneous injection.‡

3. *Effects of Suspension or Deficiency of Respiration.*

299. We have now to consider the results of the cessation of the Respiratory function, and the consequent deficiency in the supply of Oxygen and retention of Carbonic acid in the blood. If this be sufficiently prolonged, a condition ensues to which the name of *Asphyxia* has been given, the essential character of which is the cessation of muscular movement, and shortly afterwards of the Circulation; with an accumulation of blood in the venous system. The time which is necessary for life to be destroyed by Asphyxia varies much, not only in different animals, but in different states of the same. Thus, warm-blooded animals are much sooner asphyxiated than Reptiles or Invertebrata; on the other hand, a hybernating Mammal supports life for many months, with a respiration sufficiently low to produce speedy asphyxia if it were in a state of activity. And among Mammalia and Birds there are many species which are adapted, by peculiarities of conformation, to sustain a deprivation of air for much more than the average period.§ Excluding these, it may be stated as a general fact, that if a warm-blooded animal in a state of activity be deprived of respiratory power, its muscular movements (with the exception of the contraction of the heart) will cease within five minutes, often within three; and that the

* An increase of pressure was also observed by Thiry, "Zeits. f. rat. Med.," Band xxxi. p. 17; as well as G. Heidenhain, Grützner, and others, but it was not constant in the experiments of Goldstein (Pflüger's "Archiv," Band xvii. p. 343); nor by Zuntz (idem, Band xvii. p. 374).

† The beneficial results of the introduction of Mercury by inhalation are strikingly set forth in Mr. Langston Parker's Essay on "The Treatment of Secondary, Constitutional, and Confirmed Syphilis." ‡ Claude Bernard, "Leçons sur les Anæsthésiques," 1875, p. 74.

§ Thus, the Cetacea contain far more blood in their vessels than do any other Mammalia; and these vessels are so arranged, that both arteries and veins are in connection with large reservoirs or diverticula. The reservoirs belonging to the former are usually full; but when the Whale remains long under water, the blood which they contain is gradually introduced into the circulation, and after becoming venous, accumulates in the reservoirs connected with the venous system. By means of this provision, the Whale can remain under water for more than an hour.

circulation generally fails within ten minutes. In the experiments made by the Committee of the Royal Medico-Chirurgical Society,* which are corroborated by the more recent ones of M. P. Bert,† it was found that when death by drowning took place rapidly, it was due to the entrance of Water into the lungs; and that if the entrance of air into the lungs was prevented by suddenly inserting a cork into a glass tube tightly tied into the trachea, the average duration of the efforts to inspire was 4 minutes 5 seconds in dogs, and 3 minutes 25 seconds in rabbits; whilst the average duration of the heart's action was 7 minutes 11 seconds in dogs, and 7 minutes 10 seconds in rabbits. It was found also that in simple occlusion of the trachea recovery might take place after deprivation of air for 3 minutes 50 seconds, whilst immersion for 1½ min. was usually fatal.—M. Brown-Séquard‡ has shown by numerous experiments, that both newly-born animals and adults are capable of resisting the Asphyxia which results from submersion by so much longer a period as their temperature is lower, providing it does not descend below 64° F. As a general rule, the newly-born animal can survive submersion for a longer period than the adult; this, however, does not hold in the case of guinea-pigs. Of 14 newly-born rabbits submerged in water at 77° F., 5 had a temperature of 96½° F., and survived on the average 12½ minutes; 4 had a temperature of 82° to 89° F., and survived 17 minutes; lastly, 5 had a temperature of from 64° to 70° F., and these survived, on an average, 26½ minutes. A newly-born dog will survive, if its temperature be low, an immersion of 50 minutes' duration. A duck is capable of resisting the privation of air for seven or eight minutes, while a chicken will die from submersion or strangling in two or three. A satisfactory explanation of these peculiarities has been given by M. P. Bert, who has shown that they are dependent upon the amount of Oxygen in the blood, and the activity of the combustive processes in the tissues. As the blood-corpuscles constitute a magazine of Oxygen, the larger their number the longer will the animal be able to resist the privation of air; and so also life will be prolonged when from any cause the processes of oxidation in the tissues are lowered. M. Bert has elsewhere shown that the respiration of the tissues takes place less actively in young than in old animals, whilst it is obvious that a low temperature is less favourable for oxidation than a high one, and direct experiment has demonstrated that a duck contains one-third or even one-half more blood than a chicken. Many persons are capable of sustaining a deprivation of air for two, three, or even four minutes,§ without insensibility or any other injury; but this power, which seems possessed to the greatest degree by the divers of Ceylon, can only be acquired by habit. The period during which remedial means may be successful in restoring the activity of the vital and animal functions is not, however, restricted to this. There is one well-authenticated case in which recovery took place after a continuous submersion of fifteen minutes;‖ and many others

* "Trans.," vol. xlv. p. 449. † "Gaz. Médicale," 1865, p. 79.

‡ "Journal de la Phys.," vol. ii. p. 98, *et seq.*

§ Dr. Hutchinson states that any man of ordinary 'vital capacity' can pass two minutes without breathing, if he first makes five or six forcible inspirations and expirations, so as to cleanse the lungs of the old air, and then fills his chest as completely as he can. "For the first 15 seconds a giddiness will be experienced; but when this leaves us, we do not feel the slightest inconvenience from want of air." (See "Cyclop. of Anat. and Phys.," vol. iv. p. 1066.)

‖ The following are the facts of this case, as narrated by Marc ("Manuel d'Autopsie Cadavérique Médico-Légale," p. 165) on the authority of Prater:—A woman convicted of infanticide was condemned to die by drowning. This punishment was formerly inflicted in Germany according to the now obsolete Caroline law, the culprit being enclosed in a sack with a cock and a cat, and sunk to the bottom of the water. In this instance, the woman, after having been submerged for a quarter of an hour, was drawn up, and *spontaneously*

are on record, of the revival of drowned persons after an interval of half an hour, or even more; but there is not the same certainty in regard to these, that the individuals may not have occasionally risen to the surface and taken breath there. It is not improbable, however, that in some of these cases a state of Syncope came on at the moment of immersion, through the influence of fear or other mental emotion, concussion of the brain, &c.; so that when the circulation was thus enfeebled, the deprivation of air did not have the same injurious effect as when this function was in full activity. The case would then closely resemble that of a hybernating animal; for in both instances the being might be said to live very slowly, and would therefore not require the usual amount of respiration. The condition of the still-born infant is in some respects the same; its tissues, as just stated, are the seat of much less active processes of combustion than those of the adult, and re-animation has been successfully attempted when nearly half an hour had intervened between birth and the employment of resuscitating means, and when probably a much longer time had elapsed from the period of the suspension of the circulation.

300. The phenomena presented in Asphyxia,* whether produced by suddenly cutting off the supply of air, or more slowly by permitting the animal to breathe through a narrow chink, are very similar, though, in the latter case, the successive stages can be more easily followed. In the first instance there are violent inspiratory, followed after a short time by equally violent expiratory, efforts, which culminate in convulsions, the abdominal and other expiratory muscles being those chiefly affected. When the access of air to the lungs has been suddenly prevented, the expiratory convulsions, with spasms of the muscles of the limbs, occur within the first minute, and are so marked and peculiar as to have been attributed to the excitation of an expiratory convulsive centre. During this period the tension of the blood in the vessels is greatly increased. After the convulsions have lasted a few seconds they often cease suddenly, and are followed by a period of calm. The expiratory movements, in consequence of exhaustion, cease; efforts to inspire occur with long but tolerably regular intervals between them, and at each effort, when the occlusion of the trachea has been sudden, the blood-pressure falls, so that at the end of the second minute it is considerably less than natural; when, however, Asphyxia has been slowly produced, the blood-pressure as well as the frequency of the heart's beats continue to increase during this period. Reflex movements now cease, and the pupil becomes widely dilated and insensible to light. In suddenly produced and complete Asphyxia death ensues in the course of three or four minutes, preceded by inspiratory movements which are slow, feeble, and irregular, two or three efforts being made successively, followed by a long pause. In the spasms which accompany the final gasps the head is thrown back, the trunk is straightened or arched backward, and the limbs are extended, whilst the mouth gapes, and the nostrils dilate. These so-called stretching convulsions are of quite a different type from the previously mentioned expiratory convulsions. In regard to the variations of

recovered her senses. She stated that she had become insensible at the moment of her submersion; a circumstance which adds considerable weight to the supposition, based upon the post-mortem appearances in many cases of drowning, that death often takes place as much by Syncope (or primary failure of the heart's action, consequent upon sudden and violent emotion, or upon physical shock) as by Asphyxia. If the reality of this state of Syncopal Asphyxia be admitted, there does not seem any adequate reason for limiting the possible persistence of vitality in a submerged body, even to half an hour; especially if the temperature of the water be such as not to cause any rapid abstraction of its heat.

* See Burdon-Sanderson in the "Handbook for the Physiological Laboratory," 1873, p. 319, *et seq.*

the blood-pressure in Asphyxia, there appears to be a primary slight fall, followed by augmentation of the blood-pressure (in rabbits from 110 mm. to 140 mm.), which is not attributable to struggling or to the muscular movements attending the dyspnœa. It appears to be occasioned by the circulation of non-arterialized blood through the vaso-motor centre, the excitation of which causes contraction of the smaller arteries. The effect of this contraction is to fill the venous system, which becomes still more distended by the obstacle to the onward movement of the blood, presented by the contraction of the expiratory muscles of the trunk and extremities. The heart being abundantly supplied with blood fills rapidly during diastole, and contracts vigorously, in consequence of which, and of the increased resistance in front, the arterial pressure rises. This last effect is, however, temporary: the diastolic intervals being lengthened by the excitation of the inhibitory nervous system, and the heart itself weakened by defect of oxygen, the organ soon passes into a state of diastolic relaxation. Its contractions become more and more ineffectual till they finally cease, leaving the arteries empty, the veins distended, and its own cavities relaxed and full of blood. The heart's contractility is not finally lost, however, nearly as soon as its movements cease; for the action of the right ventricle may be renewed, for some time after it has stopped, by withdrawing a portion of its contents—either through the pulmonary artery, their natural channel—or, more directly, by an opening made in its own parietes, in the auricle, or in the jugular vein. On the other hand, the left ventricle may be again set in action by renewing its appropriate stimulus of arterial blood.* Hence, if the stoppage of the circulation have not been of too long continuance, it may be renewed by artificial respiration;† for the replacement of the carbonic acid by oxygen in the air-cells of the lungs restores the circulation through the pulmonary capillaries; and thus at the same time relieves the distension of the right ventricle, and conveys to the left the due stimulus to its actions. Tracings taken of the blood-pressure in gradually induced Asphyxia exhibit curves, named, after the physiologist who first observed them, Traube's curves, which indicate periodic increase and diminution of the blood-pressure, and are believed to be due either to the rhythmical stimulation of the vaso-motor centres or to the respiratory acts; inspiration favouring the passage of the blood through the capillaries of the lungs, and expiration retarding it.—Of the mode in which the pulmonary circulation is thus stagnated by the want of oxygen, and renewed by its ingress into the lungs, no other consistent explanation can be given than that which is based on the doctrine already laid down in regard to the capillary circulation in general—namely, that the performance of the normal reaction between the blood and the surrounding medium (whether this be air, water, or solid organised tissue) is a condition necessary to the regular movement of the blood through the extreme vessels. That no mechanical impediment to its passage is created (as some have maintained) by the want of distension of the lungs

* Setschenow has made some important researches on the amount and kind of gases contained in the blood of asphyxiated animals (dogs). He found that only traces of oxygen could be discovered in either the venous or arterial blood: the quantity of nitrogen varied from 1 to 2 parts, of free carbonic acid from 28 to 38·8 parts, and of combined carbonic acid from 1·7 to 4 parts (Henle and Meissner, "Bericht," 1859, p. 305).

† Of the two chief modes of performing this operation, Dr. Silvester's method of alternately raising and depressing the arms, 15 or 16 times in the minute, of which Dr. Bain's is only a modification, appears to be far preferable to Dr. Marshall Hall's method of rotating the body half over, and pressing on its chest. See Marshall Hall's work on "Drowning," "Med. Times and Gaz.," 1858, vol. i. pp. 147, 176, *et seq.*, and "Med. Chir. Transact.," vol. liii. 1870, p. 291.

has been fully proved by the experiments of Dr. J. Reid, on the induction of Asphyxia by the respiration of nitrogen; at the same time it must be admitted that the contraction of the smaller arteries is a very important factor in the arrest of the circulation in the pulmonary capillaries of the lungs, since it is in accordance with what is elsewhere seen when the vaso-motor centres are stimulated, and is very certainly deducible from the phenomena of pressure observed in the arteries and veins respectively.*

301. It is obvious that by the repeated passage of the same air through the lungs, it must, though originally pure and wholesome, become so strongly impregnated with carbonic acid, and must lose so much of its oxygen, as to be rendered utterly unfit for the continued maintenance of the aërating process; so that the individual who continues to respire it shortly becomes asphyxiated. There are several well-known cases, in which the speedy death of a number of persons confined together has resulted from neglect of the most ordinary precautions for supplying them with air. That of the "Black Hole of Calcutta," which occurred in 1756, has acquired an unenviable pre-eminence, owing to the very large proportion of the prisoners—123 out of 146—who died during *one night's* confinement in a room 18 feet square, only provided with two small windows; and it is remarkable that of the 23 who were found alive in the morning, many were subsequently cut off by "putrid fever." Such catastrophes have occurred even in this country, from time to time, though usually upon a smaller scale; there has happened one at no distant date, however, which rivalled it in magnitude. On the night of the first of December, 1848, the deck passengers on board the Irish steamer "Londonderry" were ordered below by the Captain, on account of the stormy character of the weather; and although they were crowded into a cabin far too small for their accommodation, the hatches were closed down upon them. The consequence of this was, that, out of 150 individuals, no fewer than 70 were suffocated before the morning.†

302. The determination of the cubic space which ought to be allowed for each person in workhouses, schools, and prisons, is a subject of great practical importance. It is to be borne in mind that it is not sufficient for health that a room should contain the quantity of air requisite for the support of its inhabitants during a given time only, since after they have remained in it but a part of that time, the amount of carbonic acid and other products of disintegration which its atmosphere will contain will be large enough to interfere greatly with the due aëration of their blood; but care ought to be taken that the air is renewed so frequently that the amount of carbonic acid gas does not exceed at most one part per 1000. A small room with several people in it may be better ventilated than a larger one with few inhabitants, if the provision

* For a fuller discussion of the pathology of Asphyxia, see the "Cyclop. of Anat. and Phys.," art. 'Asphyxia,' by Prof. Alison; the "Library of Practical Medicine," vol. iii., art. 'Asphyxia,' by the Author; Experimental Essays, by Dr. J. Reid, 'On the Order of Succession in which the Vital Actions are arrested in Asphyxia,' in the "Edinb. Med. and Surg. Journ.," 1841, and in his "Anat., Physiol., and Pathol. Researches;" and the Experimental Inquiry by Mr. Erichsen, in the "Edinb. Med. and Surg. Journ.," 1845.

† In Friedländer's experiments, when an animal (rabbit) was confined in a room containing a full supply of oxygen, but in which the CO_2 produced by its own respiration is allowed to accumulate, dyspnœa gradually supervened, becoming very noticeable in the course of an hour, when the amount of CO_2 reached 9 per cent. After six hours, when the proportion of CO_2 reached 30 per cent., the voluntary and respiratory movements were perceptibly weaker, and in 11 hours the respirations were only 18 per min. After 12 hours, when the amount of CO_2 had risen to 42 per cent., the animal ceased to breathe, though the heart was still beating rhythmically, and the peristaltic action of the intestines continued. (Friedländer and Herter, op. cit.)

for the renewal of the air in it be superior; and it is fortunate that a considerable amount of fresh air is introduced into all houses of modern construction by what may be termed spontaneous ventilation, as distinguished from the special arrangements made by builders and architects. This spontaneous ventilation is effected through the crevices of the doors and windows, especially when open fireplaces are used as in England, and Pettenkofer* has shown that a large and hitherto unsuspected interchange of air takes place even through the walls. Thus, in one case where the room had brick walls, and its size was 2650 cubic feet, with a difference of temperature of 34° F. (66° F. in, and 32° outside), the contents of the room changed once in one hour, a quantity of air equal to 2650 feet entering it in that time. With the same difference of temperature, but with a good fire in the stove, the communication of which with the chimney was made as free as possible, the change of the air rose to 3320 cub. feet, or about 25 per cent. When all openings, crevices in windows and doors, were thoroughly pasted up, there was still a change of 1060 feet per hour. With a difference of temperature of 7° F. (71° in, and 64° outside) the change amounted to 780 cubic feet only per hour, and when a window of 8 feet square was opened the change rose to 1060 feet per hour. These quantities are instructive: they show that a difference of temperature of 34° with carefully shut openings and crevices, is of greater influence than large communications with the outer air at a small difference of temperature, and that a large ward or room with one fireplace is not necessarily well ventilated. Pettenkofer found that in one of his rooms when the difference of temperature between the inside and outside was 9°·5 F. the spontaneous ventilation through each square yard of the wall amounted to about 7 cubic feet, or 43 gallons per hour. The material of which the wall is constructed of course exerts a great influence on the spontaneous ventilation; thus, Märker and Schultze found in their researches on the spontaneous ventilation of stables, that for one square yard of free wall at 9°·5 F. difference of temperature, the spontaneous ventilation amounted per hour—with walls of sandstone to 4·7 cub. feet, of quarried limestone to 6·5, of brick to 7·9, of tufaceous limestone to 10·1, and of mud to 14·4 cub. feet. The renewal of air should, if possible, be so regulated that no draught or sensation of air in motion is experienced. The observations of Pettenkofer and Voit made in their great apparatus at Munich show that no resistance or sense of coolness is felt at ordinary temperature if the hand be moved at a less rate than 19 inches per second, and that as a rule the motion of the air is only felt distinctly when it amounts to $3\frac{1}{4}$ feet per second. The average velocity of the air as measured by the anemometer in this climate is about 10 feet per second, which would make about 7 miles per hour; consequently in one second about 90 cubic feet, in one minute 5400 cubic feet, and in one hour 324,000 cubic feet of air flow over one person in the open. In experiments made in France in connection with the construction of the Hôpital Lariboisière, with a ventilation of 350 cub. feet per bed per hour, the smell was so bad, that the authorities at once directed the quantity to be doubled; but then also the state of air was anything but desirable, and it was only when the amount reached 2120 cubic feet per hour that the air was found to be free from perceptible taint. Pettenkofer and Voit therefore conclude that this amount of fresh air per bed per hour, representing 1-160th of the air flowing over the body in the open, is necessary for the due ventilation of hospitals, schoolrooms, &c.

* See three Lectures entitled "The Air in relation to Clothing, Dwelling, and Soil," delivered before the Albert Society of Dresden, and translated by Aug. Hess, M.D. 1874.

Pettenkofer and Voit* found that no discomfort was experienced from long exposure to an atmosphere containing 10 parts of carbonic acid in 1000 parts, providing this had been added to the air in a pure state; but if the same quantity were present as a result of the respiration of several people, serious inconvenience was soon felt; and similarly Dr. Snow observed that the presence of carbonic acid in the atmosphere acts more deleteriously upon the system in proportion as the normal quantity of oxygen is reduced. Thus, various birds and mammals introduced into an atmosphere containing only from 10½-16 per cent. of oxygen soon died, although means were taken to remove the carbonic acid set free by their respiration as fast as it was formed, whilst an increase in the proportion of carbonic acid to 12 or even 20 per cent.—the per-centage of oxygen being kept to its regular standard of 21 per cent.—did not appear to enfeeble the vital actions more rapidly than did the reduction of the oxygen in the experiments just referred to. Bernard† moreover found that a bird which lay exhausted from breathing in a limited quantity of air, recovered itself when the carbonic acid was partially absorbed by caustic potash. He observed also that the circulation of blood charged with carbonic acid rapidly arrested the activity of the secretory organs, as the kidneys, which recommenced to discharge their function as soon as oxygenated blood was allowed to pass through them. The proportion of carbonic acid present in the air of large towns has been examined by Dr. Roscoe,‡ by Dr. Angus Smith,§ and by Mr. Leigh.‖ Dr. Roscoe found the usual proportion of carbonic acid in the air of London to be 3·7 parts in 10,000; whilst the proportion in Manchester, according to Dr. Smith, was 12 parts in 10,000, on a still day, and from 4·5 to 8 parts in 10,000 on a windy day. From experiments made with permanganate of potash, he ascertained that on the high grounds north of Manchester there existed but 1 grain of organic matter in 200,000 cubic inches of air, whilst in close places in the town there was 1 grain in 8000 cubic inches. According to Braconnot,¶ the black particles always floating in the atmosphere of large towns consist chiefly of carbon, bitumen, and sulphate of ammonia. Mr. Leigh finds a small quantity of sulphuretted hydrogen in the air of Manchester. The air of sewers, and generally air loaded with organic matters, has an alkaline reaction, from the presence of ammonia and ammonium-sulphide. The average amount of CO_2 gas in the wards of London hospitals was found by Smith to be on the average 0·0781 per cent.; after midnight it rose to 0·1044, and in an overcrowded theatre it was 0·32. In New York Endemans** found: in the prisons of New York 0·083–0·152; warehouses with closed windows, 0·147–0·167; schools, both with closed and open windows, about 0·097. Theatre when full: parterre, 0·130–0·298; gallery, 0·365–0·406 per cent. The presence of a certain proportion of aqueous vapour seems to be requisite for health. F. Falk†† found that small animals, as rabbits, kept in air from which all watery vapour was withdrawn, by means of sulphuric acid and calcium chloride, soon began to breathe with difficulty, and were frequently affected by epileptic attacks; and Sanders‡‡ attributes the peculiarities of the Americans, both in mind and body, their nervous

* An abstract of these observations will be found in the "Med. Times and Gazette" for 1862, p. 459.

† Bernard, "Liquides de l'Organism," 1859, vol. i. p. 505.

‡ "Quarterly Journal of the Chemical Society," 1857; and "Med.-Chir. Review," 1861, p. 429.

§ "On the Air of Towns," quoted in "Med.-Chir. Rev.," 1861, vol. ii. p. 433.

‖ See "Twenty-ninth Annual Report of the Regist.-Gen.," 1868.

¶ "Annal. de Chimie et de Phys.," t. xxxiii.

** "Annual Report of the Board of Health, New York," 1873.

†† Virchow's "Archiv," Band lxii. 1874, p. 235.

‡‡ "Handbuch der öffentlichen Gesundsheitspflege," 1877, p. 175.

excitability, their weight, and the more rapid consumption of their vital powers to the dryness of the air in America, the prevailing s.w. wind blowing over a wide expanse of country. In Falk's experiments the saturation of the air with watery vapour produced no ill effects.

303. It appears that in all climates, and under all conditions of life, the *purity of the atmosphere* habitually respired is essential to the maintenance of that power of resisting disease, which, even more than the ordinary state of health, is a measure of the real vigour of the system. For, owing to the extraordinary capability which the human body possesses of accommodating itself to circumstances, it not unfrequently happens that individuals continue for years to breathe a most unwholesome atmosphere, without apparently suffering from it; and thus, when they at last succumb to some epidemic disease, their death is attributed solely to the latter; the previous preparation of their bodies for the reception and development of zymotic poison being altogether overlooked. It is impossible, however, for any one who carefully examines the evidence, to hesitate for a moment in the conclusion, that the fatality of Epidemics is almost invariably in precise proportion to the degree in which an impure atmosphere has been habitually respired; that an atmosphere loaded with putrescent miasmata may afford a *nidus* wherein a zymotic poison undergoes a marked increase in quantity and intensity, the putrescent exhalations from the lungs and skin of the living subject being at least as effectual in furnishing such a 'nidus,' as are the emanations from fæcal discharges or from other decomposing matters; that the habitual respiration of such an atmosphere tends to produce a condition of the blood which renders it peculiarly susceptible of perversion by the introduction of zymotic poisons, and which favours their multiplication within the system; and lastly, that by due attention to the various means of promoting atmospheric purity, and especially by efficient ventilation and sewerage, the rate of mortality may be enormously decreased, the amount and severity of sickness lowered in at least an equal proportion, and the fatality of Epidemics almost completely annihilated. The effects of good drainage and water-supply have been recently well exemplified in the case of Salisbury: the average number of deaths for the eight years preceding the completion of the drainage in this town (excluding the Cholera year) having been 27 in 1000, and for the same period since, 21 in 1000; an actual reduction of almost one-fourth of the whole number.* And it cannot be too strongly borne in mind, that the efficacy of such *preventive* measures has been most fully substantiated, in regard to many of the very diseases in which the *curative* power of medical treatment has seemed most doubtful; as, for example, in Cholera and Malignant Fevers.—The practical importance of this subject may be estimated from the startling fact, which inquiries prosecuted under the direction of the Board of Health have brought to light†—viz., that the *difference* in the annual rates of mortality, between the most healthy and the most unhealthy localities in England, amounting to no less than 34 in 1000, is almost entirely due to Zymotic diseases, which might be nearly (if not completely) exterminated by well-devised sanitary arrangements. The *lowest* actual mortality is 11 per 1000, while the *highest* is 45 per 1000; and between these extremes there is every intermediate degree of range. But what may be termed the *inevitable* mortality, arising from diseases which

* See "Times," Oct. 24, 1863.

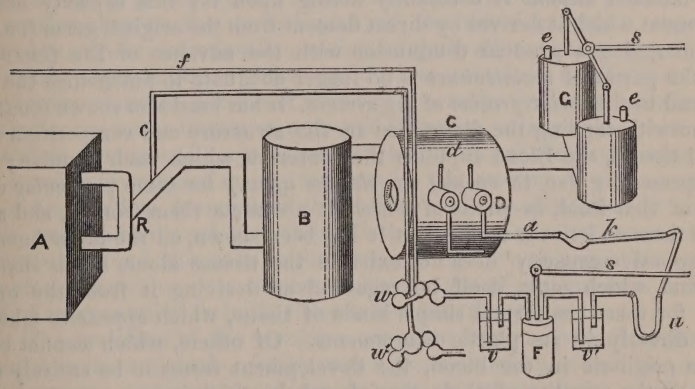
† See "Summary of Experience on Disease, and Comparative Rates of Mortality," by William Lee, Superintending Inspector, 1851. Nearly similar numbers are to be found in the "Twenty-ninth Annual Report of the Registrar-General," 1868. Of 13 large towns, the mortality of Liverpool was the highest (42 per 1000); that of Birmingham and Hull the lowest, 24 per 1000.

would not be directly affected by Sanitary improvements, is a *nearly constant* quantity throughout—namely, the 11 per 1000 of those districts which are free from Zymotic disease. The average mortality of all England, in ordinary years, is about 22 per 1000, or just double that to which it might be reduced; so that, taking the population of England and Wales (as by the last Census) at 20 millions, the average annual mortality must be 440,000, of which only 220,000 is *inevitable*, an equal amount being *preventable*.

Pettenkofer's Respiration Apparatus.

The construction of Pettenkofer's apparatus, with which so many important investigations have been made, may here be briefly given. A full description illustrated by three plates is given in the "Physiologische Chemie" of v. Gorup-Besanez. It consists essentially of a sheet-iron chamber (A), containing table, chair, and bed, from which the air is slowly exhausted by two pumps (G), worked by a small steam-engine. Fresh supplies of air are admitted through ventilators. The greater part of the air is drawn through R, and is conducted into a large receptacle (B) filled with wet pumice-stone in order to saturate it with aqueous vapour, and then enters the gasometer, where its volume is measured. From this it

Fig. 170.



is drawn by the suction of the pumps, and having passed through them escapes into the air. For the analysis of the air in the immediate vicinity of the chamber a tube (*f*) conducts a certain quantity of air which, by means of a mercurial exhausting and pressure pump (F), is drawn through the bulb apparatus containing sulphuric acid (*w*); it is then made to pass through an inspiratory mercurial valve (*v*) into F, then through a similarly constructed expiratory valve (*v'*) into the U-shaped tube (*u*), in which it is saturated with watery vapour by means of moistened pumice-stone. It is then propelled through the tube (*k*) filled with baryta water, by which the amount of carbonic acid gas present is determined. It then passes through the small meter (D), where its volume is determined, and it is finally discharged into the air through the small tube (*d*). For the analysis of the air, contaminated with the cutaneous and pulmonary excretion of the subject of the experiment, a small tube (*c*) is attached to the main discharge tube (R); the air thus obtained is conducted through a series of apparatus which is the precise duplicate of that just described, enabling an exact comparison to be instituted. The accuracy of the whole method of investigation was ascertained by control experiments with wax candles, the products of the combustion of which were compared with the amount that direct analysis showed ought to have been obtained. The average error for the carbonic acid did not exceed 0·3 per cent., and for the water 1·5 per cent. for 24 hours.

CHAPTER X.

OF NUTRITION.

1. *General Considerations.—Formative Power of Individual Parts.*

304. The function of Nutrition, considered in the widest acceptation of the term, includes that whole series of operations by which the alimentary materials—prepared by the digestive process, introduced into the system by Absorption, and carried into its *penetralia* by the Circulation—are converted into Organized tissue; but in a more limited sense it may be understood as referring to the last of these operations only—that of *Histogenesis*, or tissue-formation, to which all the other organic functions, in so far as they are concerned in maintaining the life of the individual, are subservient, by preparing and keeping in the requisite state of purity the materials at the expense of which it takes place. Every integral part of the living body possesses a certain capacity for growth and development, in virtue of which it passes through a series of successive phases, under the influence of the steady Heat, which in the warm-blooded animal is constantly acting upon it; this capacity being an endowment which it derives by direct descent from the original germ (CHAP. I.), but undergoing a gradual diminution with the advance of life (CHAP. XX.), until the power of *maintenance* is no longer adequate to antagonize the forces that tend to the *disintegration* of the system. It has been also shown (CHAP. VII.) that, notwithstanding the diversities in the structure and composition of the several tissues, the Blood supplies the materials which each require; every tissue possessing (so to speak) an *elective affinity* for some particular constituents of that fluid, in virtue of which it abstracts them from it, and appropriates them to its own uses.—But it has been shown, on the other hand, that the 'formative capacity' does not exist in the tissues alone, but is shared by the Blood, which must itself be regarded as deriving it from the original germ; for there are certain simple kinds of tissue, which appear to take their origin directly in its plastic components. Of others, which cannot be said thus to originate in the blood, the development seems to be entirely determined by the quantity of their special *pabula* which it may contain. Thus, an increase of Adipose tissue takes place, when the blood habitually includes an unusual amount of fat; an augmentation in the proportion of the Red Corpuscles of the blood may be distinctly observed (especially if it has been previously diminished unduly) when an additional supply of iron is afforded; and when one of the Kidneys has been removed, or is prevented by disease from performing its normal function, the other, if it remain healthy, undergoes an extraordinary increase in size, so as to perform the duty of both organs, the augmented development of its secreting structure being here also fairly attributable to the accumulation of its appropriate materials in the blood.* Even of those tissues which must be considered as most independent

* This principle is one most fertile in Pathological applications; for there can be little doubt that the development of many morbid growths is due, not so much to a perverted local action, as to the presence of certain morbid matters in the blood, which determines the formation of tissues that use them as their appropriate pabulum. Such is pretty obviously the case with those disorders, which (like the Exanthemata) are universally admitted to be of 'constitutional' character, and which are distinctly traceable to a poison introduced through the blood, whose first influence is exerted in modifying the physical and vital properties of that fluid: and the evidence has been of late accumulating, that it is true also of the various forms of Cancer, the local development of an abnormal structure being in this case also nothing else than the manifestation of the existence of that peculiar matter in the blood,

and self-sustaining, the development is not only checked by the want of a due supply of their appropriate materials, but it is modified in a very remarkable degree by the presence of abnormal substances in the blood, which single out particular parts, and effect determinate alterations in their nutrition, in such a constant manner as to show the existence of a very peculiar 'elective affinity' between them.—In so far, then, as the process of Nutrition is dependent upon the due supply and normal state of the Blood, its conditions have been already sufficiently discussed; and we have now only to consider it in its relations to the Tissues.

305. The demand for Nutrition primarily arises from the tendency of the organism to simple *Increase* or *Growth*. Of this we have the most characteristic illustration in the multiplication of the first embryonic cell by the simple process of "duplicative subdivision;" whereby a multitude of cells is produced, every one of which is similar in all essential particulars to the original. But after the different parts of this homogeneous embryonic mass have taken upon themselves their respective modes of development, so as to generate a diversity of tissues and organs, each one of these continues to increase after its own plan; and thus the child becomes the adult with comparatively little change but that of growth (CHAP. XVIII. SECT. 4). An excess of growth, taking place conformably to the normal plan of the tissue or organ, constitutes *Hypertrophy;* whilst a diminution, without degeneration or alteration of structure, is that which is properly distinguished as *Atrophy*.—But Growth is not confined to the period of increase of the body generally; for it may manifest itself in particular organs or tissues, as a normal operation, at any subsequent part of life; as when an extraordinary demand for the functional activity of a particular set of muscles is supplied by an increase in the amount of their contractile tissue.—And further, even where there is no such manifestation of increase, there is really a continual growth in all the tissues actively concerned in the vital operations, and this even to the very end of life; although it may be so far counterbalanced, or even surpassed, by changes of an opposite kind, that instead of augmentation in bulk, there is absolute diminution.

306. The evolution of the complete organism from its germ, however, does not consist in mere growth; for by such a process nothing would be produced but an enormous aggregation of simple cells, possessing little or no mutual dependence, like those which constitute the shapeless masses of the lowest Algæ. In addition to increase there must be *Development*—that is, a passage to a higher condition, both of form and structure; so that the part in which this change takes place becomes fitted for some special function, and is advanced towards the state in which it exists in the highest or most completed form of its specific type. Thus the development of *tissue* consists in the change from a simple mass of cells or fibres into any other form; as in the production of Dentine from the cellular substance of the tooth-pulp, or in the formation of Bone in the sub-periosteal membranes. So, again, the developmental change is seen in the passage of an entire *organ* from a lower to a higher condition, by the evolution of new parts, or by a change in the relations of those already existing, even though the change in its texture should consist of little else than of simple increase: thus, in the development of the heart, we have the original single cavity subdivided, first into two, and at last into four chambers; and in

which is the appropriate nutriment of its component tissues; or, as Mr. Simon appropriately designates it, "a new excretory organ, which tends essentially to acts of eliminative secretion, just as distinctly as the healthy liver or the healthy kidney."—See Mr. Simon's "Lectures on General Pathology," pp. 87, 152; and Sir James Paget's "Lectures on Surgical Pathology."

the development of the Brain, we find the sensory ganglia to be the parts first formed, the anterior lobes of the cerebrum to be evolved (as it were) from these, the middle lobes sprouting forth from the back of the anterior, and the posterior from the back of the middle: yet, with all this, there is no production of any new kind of tissue, the new parts being generated at the expense of histological components identical with those of the pre-existing.—Now it is in the early period of embryonic life that the *developmental* process is most remarkably displayed; for it is then that we see that transformation of the primordial cells into tissues of various kinds, which originates a special *nisus* in each part, whereby the production of the same tissue, in continuity with that first formed, comes to be a simple act of growth: and it is then also that we observe that marking out of all the principal organs, by the development of tissue in particular directions, which makes all subsequent evolution but a completion or filling-up of the plan thus sketched out. Thus, during the first days of incubation in the Chick, the foundation is laid of the vertebral column, the nervous centres, the organs of sense, the heart and circulating system, the alimentary canal, the respiratory apparatus, the liver, the kidneys, and many other parts; and at the termination of that period, the chick emerges in such a state of completeness of development, that little else than *increase* is wanting, save in the plumage and sexual organs, to raise it to its perfect type. The same may be said of the Human organism; save that the period of its development is relatively longer, in accordance with the higher grade which it is ultimately to attain; its earliest stages being passed through, however, with extraordinary rapidity. The complete evolution of the generative organs, of the osseous skeleton, and of the teeth, constitute the principal developmental changes which the Human organism undergoes in its progress from the infantile to the adult condition: almost every other alteration consisting in simple increase of its several component tissues and organs, without any essential change in their form or structure. And when the adult type has been once completely attained, every subsequent change is one rather of degeneration than of development, of retrogression rather than that of advance.

307. The difference between these two processes of Growth and Development is most characteristically shown in those cases in which there is a partial or complete arrest of one of them, without any corresponding impairment of the other. Thus a dwarf, however small in stature, may present a perfect development of every part that is characteristic of the complete human organism; the deficiency being solely in the capacity for *growth*. On the other hand, the usual size at birth may be attained, and every organ may present its ordinary dimensions, and yet some important part may be found in a condition of *arrested development;* thus the Heart may consist of a single cavity, or the inter-ventricular or inter-auricular septa may be incomplete, so that the organ has not passed beyond the grade of development which it had attained at an early period of embryonic life, although its growth may have continued; or the Brain may in like manner exhibit a deficiency of the posterior lobes, or of the corpus callosum, or of some other part whose formation normally takes place in the latter month of intra-uterine life, although the parts already produced may have continued to grow at their usual rate.—Numerous instances of the same kind might be cited, but these must suffice.

308. The demand for nutrition arises, however, not merely from the exercise of the formative powers which are concerned in the building-up of the organism, but also from the degeneration and decay which are continually taking place in almost every part of it, and the effects of which, if not

antagonized, would speedily show themselves in its complete disintegration. As each component cell of the organism has to a certain degree an independent life of its own, so has it also a limited duration; and its duration usually bears an inverse ratio to its functional activity. This is particularly striking when we compare the ratio of change in the organisms of cold-blooded animals at low and at high temperatures; for they live slowly, need little nutriment, give off but a small amount of excretory products, and require a long time for the performance of the reparative processes, under the former condition; but live fast, require a comparatively large supply of nutriment, give off a far greater amount of carbonic acid and other excretions resulting from the "waste" of tissue, and exhibit a far more rapid reparation of injuries, in the latter state. The constantly high temperature of Man, as of other warm-blooded animals, prevents this difference from being displayed in him in a similar manner; but it is well seen when we contrast his different tissues with each other, and study their respective histories. For whilst there are some (I.) which appear to pass through all their stages of growth, maturation, and decline, within a limited period, there are others (II.) whose existence seems capable of almost indefinite prolongation, and others, (III.) again, which are liable to have a period put to their life at any time, by the direction of their vital force into other channels.

I. Of those belonging to the first category, which are actively concerned in the purely *vital* operations of the organism, a characteristic example is presented by the Ovule; which, if not fertilized within a limited period after its maturation, speedily declines and decays; and the same law of limited duration doubtless extends to a large proportion of such tissues as are actively concerned in the maintenance of the organic functions; as, for example, the Corpuscles of the blood, the Epithelial cells of many glands which are instrumental in the process of Secretion, the cells forming the parenchyma of the Absorbent and Vascular Glands, and many others.

II. The contrary extreme to this may be found in those tissues whose functions are rather *physical* than vital; and especially in such as undergo consolidation by the deposit of solidifying matter, either in combination with the animal membrane or fibre, or in its interstices. Such tissues are more withdrawn from the general current of vital action; and there seems to be no definite limit to the duration of some of them, except such as is imposed by the chemical and mechanical degradation to which they may be subjected. This appears to be the case with the simple Fibrous tissues, especially the yellow, even in their soft or unconsolidated state; but it is far more obvious in the dentine and enamel of Teeth, which are formed by the combination of calcareous salts with an animal matrix, and which retain their condition apparently unchanged through the whole remainder of life, under circumstances which show that if any nutritive action takes place in them, its amount must be extremely small. In the dentinal structure of the young, however, there is obviously a determinate limit of existence; as is shown by the exuviation, at a certain definite epoch, of the first set of teeth, which exuviation is usually preceded by the death and partial disintegration of their texture. In Hair, Nails, and other Epidermic appendages, again, whose substance, when once it has undergone consolidation by the deposit of horny matter, may remain unchanged for centuries, we must recognise the same principle of indefinite duration, in connection with the cessation of vital activity; the chemical constitution of these textures, moreover, being such as renders them but little prone to be acted upon by ordinary decomposing agencies. The limit of existence seems more determinate, however, in Bone; for not only do we find that, in the first development of this substance, a considerable part of the

tissue originally generated by the consolidation of its osseous or cartilaginou matrix speedily disappears, and that during the whole period of growth of th shaft of a round bone, there is a continual removal of its inner and olde portions, whereby the medullary cavity is progressively enlarged ; but there i strong evidence that, even after the bone has attained its full dimensions a replacement of old Haversian systems by new is continually in progress.

III. In the case of the Muscular and Nervous tissues, however, we trace the operation of causes that differ from any of those already specified. These tissues are doubtless subject, like all others that are distinguished by their vital activity, to the law of limited duration; for we find that, when not called into use, they undergo a gradual disintegration or wasting, which is not adequately repaired by the nutritive processes. But their existence as living structures appears to be terminable at any time, by the exercise of their functional powers; for the development of muscular contractility or of nervous force seems to involve, as its necessary condition, a metamorphosis (so to speak) of the vital power which was previously exercising itself in the nutritive operations; and the materials of these tissues, now reduced to the condition of dead matter, undergo those regressive changes which speedily convert them into excrementitious products. But the very manifestation of their peculiar vital endowments determines an afflux of blood towards the parts thus called into special activity; and from this it comes to pass, that the nutrition of these textures is promoted, instead of being impaired, by the losses to which they are thus subjected; so that their constant exercise occasions an augmentation rather than a diminution of their substance—a due supply of the requisite materials being always presupposed.

309. Thus it comes to pass, that, during the whole period of active life, a demand for Nutrition is created by every exertion of the vital powers, but more especially by the evolution of the Nervous and Muscular forces. The production and application of these, indeed, may be considered as the great end and aim of the Human organism, so far at least as the individual is concerned; the whole apparatus of Organic life being subservient to the building up and maintenance of the Nervo-muscular apparatus, and of those parts of the fabric (*e.g.*, the bones, cartilages, fibrous textures, &c.) which it uses as its mechanical instruments. Thus the activity of all the Organic operations, when once the full measure of growth has been attained, is mainly determined by that of the Animal functions; and as the "rate of life" of all the parts which minister to the former will be proportioned to the energy with which they are called upon to perform their functions, their duration will diminish in the same proportion, and hence occasion will arise for their continual renewal.* But since,

* Such an excellent illustration is afforded by the phenomena of Vegetation, of the doctrines here propounded, that it scarcely appears desirable to pass it by in this place, although it has been elsewhere more fully referred to (PRINC. OF COMP. PHYS., §§ 265, 358). —The leaves of Plants serve, like the absorbing and assimilating cells of Animals, for the introduction and elaboration of the nutritive materials which are to be applied to the extension of the fabric; the more permanent and inactive parts of which are thus generated at the expense of materials prepared by the vital operations of the more transitory and energetic. Now there is an obvious limit to the duration of the leaf-cells; but this limit is not precisely one of *time*, being rather dependent upon the *completion of their series of vital actions*. Thus, although we are accustomed to look upon the 'fall of the leaves' (which is nothing else than an exuviation consequent upon death) as a phenomenon of regular seasonal recurrence, and to regard their replacement by a new growth as occurring at a not less constant interval, yet experience shows that these intervals are entirely regulated by temperature; for if one of the ordinary deciduous trees of temperate climates be transferred to a tropical climate, it will live much faster, its leaves being shed far more frequently, and being replaced much more speedily; so that two, or even three, successive exuviations and reproductions of its foliage may take place within a year.

in the attainment of the adult condition, the productive capacity has undergone a gradual diminution, whilst the exercise of the animal powers has become vastly increased, the formative processes are only capable of *maintaining* the Organism in its state of completeness and vigour by making good the losses consequent upon the continual disintegration to which it is subjected by its nervo-muscular activity. And with the advance of years, the further diminution of the productive capacity involves—on the one hand, a progressive decrease in the substance of the tissues and organs most important to life (their bulk, however, frequently remaining unchanged, or even increasing, in consequence of the accumulation of fat)—and on the other, a gradual weakening of its power of action. (See CHAP. XX.)

310. The performance of the function of Nutrition, the demand for which arises out of the causes that have been now discussed, is dependent, not merely upon a due supply of pure and well-elaborated blood, but also upon the normal condition of the part to be nourished, and especially upon its possession of a right measure of "formative capacity;" in virtue of which the newly-produced tissues are generated in the likeness, as well as in the place, of those which have become effete. The exactness of this replacement is most remarkably shown in the retention of the characteristic form and structure of each separate organ or part of the body, and thus of the entire organism, through a long series of years; no changes being apparent (so long as the state of health is preserved), but such as are conformable to the general type of that alteration which the organism undergoes with the advance of life. And not only is this to be noticed in the conservation of all those distinguishing points of structure which mark the species and are essential to its well-being, but it is still more remarkably displayed in the continuous renewal of those minor peculiarities which constitute the characteristic features of the individual, and which serve to distinguish him from his fellows. And how much this depends upon the formative capacity originally derived from the germ is evident from this, that a similar moulding (so to speak) of the nutritive material takes place, in its original development, at first into the form characteristic of the species, and afterwards into that which marks the individual; and that the peculiarities of the individual are frequently such as have been distinctive of one or other of the parents, or present a combination of both. But it is curious that the formative power should often be exercised, not only in maintaining the original type, but also in keeping up some acquired peculiarity; as, for example, in the perpetuation of a cicatrix left after the healing of a wound. For, as Sir J. Paget has remarked, the tissue of a cicatrix grows and assimilates nutrient material, exactly as do its healthy neighbouring tissues; so that a scar which a child might have said to be as long as his own forefinger will still be as long as his forefinger when he becomes a man. And when the mode of nutrition in any part has been altered by disease, there is frequently an obstinate tendency to the perpetuation of the same alteration; or, if the healthy action be for a time restored, there is a peculiar tendency to the renewal of the morbid process of the part; and this is stronger the more frequently it recurs, until at last it becomes inveterately established. There is, however, in the Tissues generally, as in the Blood, a general tendency to a return to the normal type after it has undergone a temporary perversion; and thus it is that we find the typical structure of parts generally restored when the morbid tendency has been overcome; and that even cicatrices and indurations, notwithstanding their usual obstinate persistence, occasionally disappear. The normal type is, perhaps, less likely to be thus recovered when the departure from it is very slight, and consists rather in the wrong plan (so to speak) on which the

new matter is laid down than in a perversion of the nutritive process itself. It may be useful to conclude this section with a table showing the proportion which the several component parts of the body bear to one another.* It will be seen how large a percentage of the body is composed of the soft tissues, in which rapid processes of disintegration and reconstruction are constantly in course of performance:—

——	Man æt. 33, executed.	Woman æt. 22, killed by accident.	Youth; suicide.	New-born.		Fœtus, sixth month.
				Boy.	Girl.	
Weight of the whole body in grammes	69,668	55,400	35,547	2400	2969	643
Percentage proportion of—						
Skeleton	15·9	15·1	15·6	17·7	15·7	20·3
Muscles	41·8	35·8	44·2	22·9	23·9	22·3
Thoracic Viscera .	1·7	2·4	3·2	3·0	4·5	2·7
Abdominal Viscera .	7·2	8·2	12·6	11·5	12·1	12·3
Fat	18·2	28·2	13·9	20·0	13·5	14·8
Skin	6·9	5·7	6·2		11·3	
Brain	1·9	2·1	3·9	15·8	12·2	18·5

The proportion of water in the body of adults is about 58·5 per cent.; in the new-born child, 66·4 per cent.; the muscles contain 75·7 per cent.; the fat, 29·9; the skin, 72; the blood, 83; the liver, 69·3; and the brain, 75 per cent. of that fluid.

2. *On the Balance of the Vital Economy, or the Relations which subsist between the Ingesta, the Metamorphosis of Tissue, the Work accomplished in and by the Body, and the Ingesta.*†

311. During the last few years many laborious investigations have been undertaken, with a view to determine what may be called the "balance of the vital economy;" or, in other words, to ascertain not only the kind and quality of food requisite to maintain life under varying external conditions, but to gain an insight into the manner in which different kinds of foods are applied to the formation of tissue, the production of mechanical force, and to the maintenance of animal heat; and also the mode in which the results of their metamorphosis within the body are ultimately discharged by the various excretory organs. The average amount of food required by the body has already been given (§ 68), and it has been shown that the ordinary diet of the working man contains between 250 and 300 grains of nitrogen, and between 4000 and 5000 grains of carbon; that he consumes besides about five pints of water and a very variable quantity (200–600 grains) of salts; lastly, that

* From Ranke, "Grundzüge der Physiologie," 1868, p. 143.

† The following are some of the more important recent works on this subject:—Bidder and Schmidt, "Die Verdauungssäfte und der Stoffwechsel," 1852. Lawes and Gilbert, "Philosoph. Trans.," 1859. Bischoff and Voit, "Die Gesetze der Ernährung des Fleischfressers," Leipzig, 1860. Henneberg and Stohmann, "Beiträge zur Rat. Futterung der Wiederkauer," Braunschweig, 1860. Ranke, "Archiv f. Anat. und Phys.," 1862. Pettenkofer and Voit, "Annal. d. Chemie und Pharmacie," 1862. Schützenberger, "Chimie appliqué à la Physiologie." Seegen, "Sitz.-ber. d. Wien. Akad.," Band lv. lxiii. 1871. Voit in "Zeits. f. Biologie," Band ii. 1866, pp. 6 and 289, Band iii. 1867, p. 1, Band iv. p. 517 ("über Luxus Consumption"), and his experiments either alone or in conjunction with Pettenkofer in the succeeding six volumes of this periodical, which contains numerous other articles on this subject by different workers. See also North, "Urea and Muscular Labour," Foster's "Journal of Physiology," vol. i. p. 171, 1879.—The Editor must here acknowledge his obligations to the standard works of Funke, Ludwig, Vierordt, Budge, Longet, Milne-Edwards, Wundt, Herrman, and Ranke; in each of which, excellent sections on "Nutrition" will be found.

he requires about 11,000 grains of oxygen. These collectively constitute the *Ingesta.* The *Egesta* are represented by the excretions of the Kidneys, Bowels, Lungs, and Skin,* which are composed of the more or less completely oxidized constituents of the food and tissues, as well as, in the case of the alvine evacuations, of the indigestible residue of the food. If the weight of the body remain stationary, the Egesta must necessarily be precisely equal to the Ingesta. But if the quantity of food consumed be greater than necessary, then one of several events may occur: either it fails to be absorbed, and is simply discharged by the bowels, as in an experiment of Ranke, who found that with 64 oz. of meat 22¼ oz. were thus eliminated unaltered; or (as in the case of water and salts) it may be absorbed, and be immediately discharged by the kidneys and skin; or it may be absorbed and be deposited in the body (as often occurs with fat), increasing its weight; or, lastly, it may minister to the performance of more work, and after undergoing oxidation may increase the Egesta generally. If, again, the supply of food be insufficient in quantity, the weight of the body must diminish, the excreta remaining the same, or, the weight of the body being maintained, the excreta must diminish. Speaking generally, increased demand for food and increase of the Egesta are associated with increased activity of the cell-functions throughout the body, which may express themselves in the formation of more abundant secretions, the more rapid circulation of the blood, and the greater energy of the nervo-muscular apparatus. Bidder and Schmidt estimate that the respective amounts of the various digestive fluids which are daily poured into the alimentary canal of an adult Man weighing 14 stone, are nearly as follows:—

	oz.		grains.	
Saliva	56·8	containing	233	of solid matter.
Bile	56·8	„	1208	„
Gastric juice	147·2	„	2976	„
Pancreatic fluid	7·1	„	310	„
Intestinal juice	7·1	„	46	„

So that nearly 10 oz. (*troy*) of solid matter are separated from the blood in the digestive secretions, for the purpose of introducing new alimentary materials of not more than two or three times the amount; and thus we see that a large portion of the food ingested and assimilated must be consumed in providing for the introduction of a further supply, in addition to that which, when duly assimilated, is applied by the nutritive processes to the repair of the solid tissues. All these processes imply the more active absorption of oxygen and a corresponding increase in the excreta, which are essentially products of combustion, so that when the muscles are powerfully exerted, larger quantities of carbonic acid and water are excreted, whilst if the activity of the glands is increased, more urea (containing the chief portion of the nitrogen of the ingesta) is eliminated. It must be understood, however, that it is not owing to the quantity of oxygen absorbed that the general activity of the cells throughout the body is augmented, but the activity of these regulates the amount of oxygen absorbed. This is well shown by the fact that whilst, as Ewald has pointed out, the oxygenation of the Hæmoglobin may be raised to saturation by sufficiently active respiration, this does not lead to any increase in the consumption of oxygen by the economy (Pflüger). To augment the consumption of oxygen, the growth and multiplication and functional activities of the cells of the organism must be increased. These activities are dependent upon the play of molecular forces in the cells—that is to say, upon the entrance

* To which may be added the fluids discharged at certain periods by the Mammary Glands, Testes, and Uterus.

into and exit of nutritive fluids from their interior, and the changes effected by the cells in such fluids and on their own composition. Albumin, when abundantly supplied, augments these changes. Fats and sugars diminish them, and they fall to a minimum in inanition. Voit has with some success endeavoured to establish a distinction between "circulating albumin" and "tissue" or "organ albumin," the former of which supplies the new material required to replace the old in cell-formation, and is much more susceptible of the action of oxygen. He estimates, indeed, that of the tissue-albumin only one per cent. is destroyed, whilst about 70 per cent. of the "circulating albumin" undergoes disintegration. Voit supports his views by a comparison of the amount of albumin decomposed in inanition with that in excessive consumption of meat, in which it may be as much as ten times greater. The following experiment by Pettenkofer may be selected as an example of the mode in which the balance of the Ingesta and Egesta is worked out in the apparatus he has constructed for the purpose, and a description of which has already been given (p. 395).* In considering experiments of this nature, it may be accepted as a fact that all the nitrogen of the food is eliminated by the urine and fæces; the quantity discharged by the lungs and skin (0·6 of a grain in 24 hours) being too small to interfere with the results (Parkes). The subject of the experiment was a strong and lively dog, weighing 33 kilogrammes (or 72 lbs., the kilogramme being 2·2 lbs. avoird.), which was found to maintain its weight nearly unaltered when fed with 1500 grammes (23,160 grains, the gramme being 15·44 grains) of meat per diem; whilst thus fed it absorbed from the air 477·2 grammes (7367 grains) of oxygen. Analysis of the excreta gave the following results:—

Ingesta.		*Egesta.*	
Meat	1500 grammes	Urine	1075·0 grammes.
Oxygen	477·2 „	Fæces	40·7 „
		Carbonic Acid	538·2 „
		Water	354·8 „
		Carburetted Hydrogen	1·6 „
		Hydrogen	1·4 „
	1977·2		2011·7

Analysis of the *Ingesta* showed that—

1500 grammes of meat contained		187·8 grammes	of Carbon.
„ „ „ „		152·45 „	of Hydrogen.
„ „ „ „		51·0 „	of Nitrogen.
„ „ „ „		1089·25 „	of Oxygen.

Of the 1089·25 grammes of Oxygen 77·25 were contained in the dry meat and 10·12 in the water, and of the 152·45 grammes of Hydrogen, 25·95 were contained in the dry meat and 126·50 in the water. In addition, 477·2 of Oxygen were absorbed from the air. The total ingestion of Oxygen was therefore 1566·45 grammes.

Analysis of the *Egesta* showed 1075 grammes of urine, containing, with 152·2 of dry residue, 107·9 grammes of urea and 16·3 grammes of salts. After deducting the urea and salts from the total residue there remained for other urinary constituents 28 grammes, which further analysis showed to contain 9·6 grammes of carbon, 2·5 grammes of hydrogen, and 15·9 of oxygen: 40·7 grammes of moist fæces, which when dried weighed 11·2 grammes, contained 4·9 grammes of carbon, 0·7 of hydrogen, 0·7 of nitrogen, 1·5 of oxygen, and 3·4 grammes of salts. We have thus in the Egesta—

* V. Gorup-Besanez, "Lehrbuch der Physiologischen Chemie," 1875, p. 843.

Carbon	21·6	grammes	contained in the urea.
„	9·6	„	„ in the other constituents of the urine.
„	4·9	„	„ in the fæces.
„	146·7	„	„ in the carbonic acid gas of the pulmonary and cutaneous transpiration.
„	1·2	„	„ in the marsh gas of the pulmonary and cutaneous transpiration.
Total . .	184·0	grammes.	

Hydrogen . . .	7·2	grammes	contained in the urea.
„ . . .	2·5	„	„ in the urinary constituents.
„ . . .	102·5	„	„ in the water of the urea.
„ . . .	0·7	„	„ in the dry fæces.
„ . . .	3·2	„	„ in the water of the fæces.
„ . . .	39·4	„	„ in the water of the transpiration.
„ . . .	0·4	„	„ in the marsh gas of the transpiration.
„ . . .	1·4	„	„ in the hydrogen of the transpiration.
Total . .	157·3	grammes.	

Nitrogen . . .	50·4	grammes	contained in the urine.
„ . . .	0·7	„	„ in the fæces.
Total . .	51·1	grammes.	

Oxygen . . .	28·8	grammes	contained in the urea.
„ . . .	15·9	„	„ in other urinary constituents.
„ . . .	820·3	„	„ in the water of the urine.
„ . . .	1·5	„	„ in the dry fæces.
„ . . .	26·3	„	„ in the water of the fæces.
„ . . .	391·5	„	„ in the carbonic acid of the pulmonary and cutaneous transpiration.
„ . . .	315·4	„	„ in the water of the transpiration.
Total .	1599·7	grammes.	

Salts	16·3	grammes	contained in the urine.
„	3·4	„	„ in the fæces.
Total .	19·7	grammes.	

If the Ingesta and Egesta are now briefly compared, we get the following balance :—

	Ingesta.	*Egesta.*
Carbon	187·8	184·0
Hydrogen	152·5	157·3
Nitrogen	51·0	51·1
Oxygen	1566·4	1599·7
Salts	19·5	19·7
	1977·2	2011·8
Difference	34·6 grammes.	

The excess of the Egesta over the Ingesta is nearly 35 grammes; this amounts to not quite 1 per cent. of the total weight of the Ingesta and Egesta. This excess is believed by Pettenkofer and Voit to be attributable to the excretion of a small quantity of water, which is rendered probable because the excess of oxygen and hydrogen is in the proportion in which they form water, and because if from the actual body weight the mean daily quantity of fæces was deducted, there was an actual diminution in the weight of the animal amounting to 34 grammes. The minus quantity of 3·8 grammes of Carbon they attribute to a small production of fat from the meat. Numerous experiments of a similar nature have been made on the same principle on man and animals by Pettenkofer and Voit. The principal source of error in experiments con-

ducted in this manner lies in the analysis of the flesh administered as food, especially in regard to the nitrogen which it contains. The estimate here taken was that of Voit,* who considered it to contain 3·4 per cent. of nitrogen; but other observers† have found that the proportion varies in the flesh of different animals, or when the composition of the flesh is determined by different methods of analysis, from 2·14 to 5·17 per cent., so that a surplus or a deficit of nitrogen would be found in the excreta according as the one or the other estimate is taken as the average. Another difficulty is in the analysis of the fæces, especially when the experiment is made on one of the herbivora or on an omnivorous animal, on account of the large amount of indigestible material they contain. In the carnivora, on the other hand, the amount of indigestible substances is insignificant. Thus in cats it does not exceed one per cent. (Bidder and Schmidt); in man it amounts to 4–8 per cent. (Valentin, Barrel, Hildersheim), in the pig to 19·9 per cent. (Boussingault), in the cow to 34·4 to per cent. (Boussingault), and in the horse to 40–50 per cent. (Valentin).

312. *Balance of the Economy in Fasting.*—Great interest attaches to the study of the excreta during inanition, for we may be sure, from the care that we elsewhere see to be taken by Nature in the preservation of life, that the animal then lives most economically; for it is, in fact, living upon its own tissues, and no more is consumed than is absolutely requisite for the maintenance of the internal work of the body, which becomes greatly reduced in amount, whilst after the first day or two there is little disposition to external work. The chief objection to this method of determining the minimum quantity of food required and the minimum amount of Egesta discharged from the body is, that soon after the withdrawal of all supplies, the activity of the principal organs, as the liver, pancreas, spleen, glands of intestine, &c., undergoes material diminution. The diminution in the general weight of the body and of the several excreta begins on the very first day of fasting, and continues throughout, though of course, in consequence of the progressively smaller bulk of the body, in a gradually lessening proportion. The most marked alteration in the excreta occurs in the herbivora, since in fasting they live on themselves; in other words, change from a vegetable to an animal diet, and the urine consequently contains for a time an increased proportion of nitrogen. Both in these animals, however, and in carnivora, the amount of urea gradually diminishes with the diminished bulk and lessened external and internal activities. Well-fed animals bear inanition for a longer period than ill-fed ones, —lean young pigeons dying in three days, and after a loss of only a fourth of their weight, whilst old, well-nourished ones live for thirteen days, and do not die till their weight is reduced to one-half. The loss of weight falls very unevenly on different organs, the store of fat, for example, being almost entirely used up, whilst the nerve-centres undergo scarcely any change; from which it would appear that some organs continue to be nourished at the expense of others. Ranke gives the following as the results of an experiment upon himself, in which no food or drink was taken :—

Body weight before the experiment	69,643	grammes.
„ after „	68,513	„
Loss .	1,130	„

* Voit, "Zeits. f. Biologie," Band i. p. 100.

† Nowak, Leube, Siëwert, Petersen, Ritthausen, "Zeitschrift f. Biologie," Band vii. 1871. Seegen, "Wien. Akad. Anzeiger," 1870, p. 230. Schenk, "Sitzungsber. d. k. Akad. zu Wien." Jan. 1870.

The ingesta (*i.e.*, loss of weight of the body) were calculated for twenty-four hours of the second day of total abstinence from the loss of weight of the body :—

Egesta.	N.	C.	*Ingesta.* (Estimated)	N.	C.
17·025 Urea	7·9455	3·5654	50·7 grammes of Albumen . .	8·024	27·796
0.236 Uric acid . .	0·0786	0·0843			
In the respiration . .	0·	180·8500	198·1 grammes of Fat	0·	156·700
Total .	8·024,	184·5		8·024	184·5

The calculated loss of albumin and fat amounted to 248·8 grammes, to which must be added 7·7 grammes of extractives and salts excreted in the urine. The loss of solids amounted to 256·5 grammes; the remainder, therefore—873·5 grammes of the total loss—was water. Seegen,* from the amount of N. eliminated in the urine, found that in a young girl, who, in consequence of stricture of the œsophagus, was only able to swallow about an ounce of milk per diem, the consumption of body albumin, reckoned dry, was about 386 grains per diem, and that, since an excess of water was egested, the blood and tissues must have become poorer in water, or drier. The metamorphoses of the albuminates during fasting, so far as they were represented by the excretory products of the urine, bore the proportion to the normal metamorphosis of 1 : 4 or 1 : 5. It must be borne in mind, however, that we cannot conclude from analysis of egesta in the fasting state, or from calculation based on those analyses of the quantity of albumin or fat actually consumed in the acts of life, that we have obtained accurate data of the minimum required for the maintenance of an animal in its normal state; for numerous experiments have shown, that if the same amount of food be given as will exactly cover egesta in the fasting state, the excretions by skin and lungs, urine and fæces, will exceed that quantity in weight; clearly showing that the animal still consumes a portion of its own body, or, in other words, that more than a minimum is required. According to Bidder and Schmidt, whilst the loss of weight sustained in a cat during inanition is about 2·2 per cent. daily, nearly twice as much, or 4·4 per cent., is required to keep up its weight to the ordinary standard. The most important of the conclusions drawn by Schmidt in regard to the effects of fasting are—1. That whilst the daily quantity of fat undergoing oxidation, in a fasting animal, remains nearly constant; that of the albumin falls in the course of the first two days to one-half, then remains constant for eight days, then falls slowly, and during the last two days diminishes rapidly and considerably. 2. The quantity of expired aqueous vapour diminishes continually, but unequally, falling more quickly at the commencement and at the end of the experiment. The proportion of aqueous vapour eliminated by the skin and lungs to that discharged by the urine and fæces remains constant as 10 : 7. The absorption of oxygen is also found to diminish unequally, being much less at the commencement of the period of inanition and towards the close of life. The quantity of oxygen expired as carbonic acid also falls (from 80 to 73 per cent.). On the whole, a fasting animal loses daily 1 per cent. of its body substance, calculated *as free from water*, of which 0·6 is albuminous and 0·4 fat. Bischoff and Voit have made similar series of researches on a dog, after having previously in one experiment fed it well; in a second, after having gradually diminished the amount of food; and in others, after having given it an excessive supply of meat and fat. The general conclusions at which they arrived were, that during inanition the

* Seegen, loc. cit., and abstract in "Lancet," 1871, vol. i. p. 793.

amount of consumption of the animal's own tissue was dependent upon its size; since if it had been previously well fed, it lost more in a given time, and if it had been badly fed, it lost less; living in the latter case, as it were, more economically. And further, the consumption was found to fluctuate between the two chief factors of the body—the muscular tissue and the fat—in such a manner that a very muscular animal consumed more flesh, and a very fat animal more fat; which result is attributable in part to the presence of a greater bulk or mass of the tissue, which is consequently more exposed to the action of the oxygen absorbed, and undergoes a greater amount of disintegration. In the experiment in which the animal had been previously well fed, and with a mean weight of 70 lbs., the proportion of nitrogen to that of carbon eliminated was as 1 : 19; the proportion of nitrogen eliminated per diem for each 1 lb. of body weight being 2·1 grains, and of carbon 40 grains. In a second experiment, where the dog had previously been fed on progressively-diminishing quantities of meat, and weighed 70·7 lbs., the proportion of N. to C. was as 1 : 24, and there were eliminated for each 1 lb. of body weight 1·68 grains of N. and 40 grains of C. In a third experiment, where the dog had been so abundantly fed that its mean weight throughout the experiment was 85 lbs., the proportion of N. to C. was as 1 : 16·3, the quantity of N. eliminated per diem to each 1 lb. of body weight being 1·54 grains, and 25·2 grains of C.—Similar observations have been made by Ranke* on himself; and the influence of diet in Man, in effecting a variation in the composition of the excretions, is well shown in the following Table, based on his experiments:—

	Proportion of Nitrogen to Carbon in the collective excretions of the Skin, Lungs, and Kidneys.	Quantity of Nitrogen excreted per diem for each 1 lb. of body weight, in grains.	Quantity of Carbon excreted per diem for each 1 lb. of body weight, in grains.
With mixed food	1 : 12	1·817	45·7
In inanition	1 : 17	1·000	17·82
With non-nitrogenous food	1 : 25	·788	19·5
With excessive and exclusive meat diet (4 lbs.)	1 : 6	8·670	52·8

Ranke found in his experiments that Man required more carbon, *i.e.*, more fat or starch, in his food to supply the wants of his economy, than appeared to be requisite in the Dog experimented on by Bischoff and Voit; and he further remarks that the quantity of nitrogen appearing in the excreta bears an inverse proportion to the carbon contained in the food: consequently, when the fat or starchy constituents of the food are insufficient, the albuminous constituents of the body are drawn upon or are consumed to maintain the temperature. He found also—1. That the minimum quantity of urea (containing nearly all the nitrogen) is discharged during hunger. 2. That whilst mere increase in the quantity of food, irrespective of its composition, has no effect in increasing the quantity of nitrogen eliminated by the kidneys, an increase in the proportion of nitrogenous diet is followed by an increased discharge of urea, though this does not rise proportionately for 24 hours at least; the effect, however, enduring for some time after the withdrawal of such food. 3. The same holds with regard to uric acid. In fasting animals Voit found the proportion of water in the several organs increased in amount, so that in a starved cat the percentage of water in the muscles was 76·5 per cent., whilst in a well-nourished cat it only amounted to 74·6 per cent.; and Ranke found that in the muscles of Frogs in winter, when they obtained little or no food, the proportion

* Müller's "Archiv," 1852, p. 335, *et seq.*

of water was 83 per cent., whilst in summer, when they were well fed, it was only 79. Such increase of the proportion of water has a powerful effect in exhausting the muscles, and probably also leads to depression of the temperature by interfering with the processes of oxidation.

313. The conclusions arrived at by Bischoff and Voit upon the effect of feeding their Dog on pure meat diet are especially interesting. They found that, in order that the animal should neither lose nor gain in weight, a daily supply of meat equal to from 1-20th to 1-25th of the whole weight of its body was required (a smaller proportion than that found requisite by Bidder and Schmidt in the experiments on the Cat); and that if less than this were supplied, a loss of weight took place in consequence of the animal consuming some of its own flesh and fat; whilst if more than this proportion were supplied, a gain in weight occurred. But to produce a daily increase in weight—a constantly increasing weight—a relatively larger proportion of food was continually required, until at last a maximum was attained; the animal then loathed its food, consumed no more, and rapidly returned to its standard weight. At the same time they found that the quantity of meat which the dog required to cover loss on the one hand, and to form flesh on the other, varied always with the mass of the body. In the well-fed animal, therefore, it required more, in the badly-fed less, to produce the same effect. They further conclude that when large quantities of meat are consumed, the products of its retrogressive metamorphosis take up or combine with the oxygen of the blood, and that thus the fat of the animal is spared; the animal's temperature being sufficiently maintained by the combustion of the secondary products of the disintegration of the albuminous compounds. Each animal has a maximum limit of alimentation, which cannot be passed without inducing disturbance of the general health, and this limit varies for each kind of aliment. It is easily reached in the case of fats and albuminoids, but only with difficulty in the case of fats and water.

314. These results have been verified by Ranke in experiments upon himself, with the exception that he found that he was unable to subsist entirely upon a meat diet, and still less, as Hammond has already shown (§ 62), upon pure albumen. Large supplies of meat with diminution of hydrocarbonaceous compounds invariably diminished the fat of the body. The method of diminishing excessive obesity suggested by Mr. Banting, and which consisted in augmenting the use of flesh and reducing the consumption of farinaceous and oleaginous food to a minimum, is founded, therefore, on strict physiological principles. The economy that is effected by a varied diet, and the immense loss of material that results from restricting man to an exclusively animal diet, have already been fully dwelt upon (CHAP. V.). An extraordinary amount of albumen undergoes disintegration on a pure meat diet. Thus Ranke* found that, whilst a healthy man ordinarily excreted about 570 grains of urea per diem, the amount rose to 1327 grains per diem on a pure flesh diet, and he draws particular attention to the fact, that, so far from the increased excretion of urea being due to augmented muscular work, the first effect of an excessive meat diet is not that of increased strength, but rather a feeling of heaviness and weariness in the muscles, with nervous excitation, often rising to sleeplessness, which he attributes to the accumulation in the blood of the alkaline salts of the meat. The following gives the result by Ranke of an experiment on his own person in Pettenkofer's Respiration Apparatus when consuming as much pure flesh as possible:—

* Ranke, "Grundzüge der Physiologie," 1874, p. 196.

Initial weight . . 72·927 kilogrammes.
Terminal weight . 72·781 „
Difference: a loss of weight of 146 grammes, notwithstanding the large amount of meat consumed.

Ingesta.	N.	C.	*Egesta.*	N.	C.
1832 grammes of meat	62·29	229·36	86·3 grammes of urea	40·28	17·26
70 „ of fat	0·	50·27	1·95 „ of uric acid	0·65	0·70
31 „ of salts			99·0 „ of fæces .	3·26	14·88
3371 c. c. of water.			In the respiration . . .	0·	231·20
			2073 c. c. urine.		
			26·6 grammes of common salt.		

The difference in the amount of N. (= 18·1 grammes in favour of the ingesta,) shows that about 523 grammes of albumen were retained in the body, and in order to cover the egesta about 23 grammes of fat must have been supplied by the body. The result of the addition of fat to the food of a carnivorous animal was found by Bischoff and Voit materially to diminish the disintegration of albuminous compounds, as shown by the diminished elimination of urea, so that only a third or fourth part is required. This is intelligible enough when it is remembered that only a certain quantity of ozonized oxygen is present at any moment in the body, and that, since the hydrocarbons possess a much higher affinity for oxygen than the albuminous compounds, they essentially spare or prevent the disintegration and oxidation of the latter. They do not, however, interfere with the ordinary decomposition and reconstruction of the muscular tissues. But if, with the fat, an increased proportion of meat be given, the proportion of urea also increases, obviously because when much more albuminous material is contained in the blood than is required for the maintenance of the tissues, and especially of the muscles, it undergoes oxidation, and, instead of being applied to the tissues, is used up for the production of heat. Sugar and starch consumed with a meat diet seem to operate in precisely the same manner as fat, except that their action, in combining with oxygen, and thus sparing both the adipose and nitrogenous compounds, is, in consequence of their greater affinity for oxygen, still more marked than fat; and if large quantities of sugar be given with sufficient albumen, a deposition of fat invariably takes place.

315. The differences which exist between Carnivora and Herbivora, in regard to the mode in which the constituents of the Ingesta are distributed through the excretions, are very striking. The first and most remarkable feature of difference between them is the very large proportion which the fæcal discharges of the Herbivora bear to the other excretions, which obviously proceeds from the indigestibility of a large part of the alimentary substances they consume. Of the *water* taken into the alimentary canal or formed within the body, nearly two-thirds pass off with the fæces in the Horse, whilst nearly the whole is absorbed in the Cat; and of that which is absorbed by the Horse, little more than one-seventh passes into the urine, the remainder being exhaled from the lungs and skin; whilst in the Cat, the proportion which passes off by the skin is less than one-sixth of that which is absorbed, the remainder being eliminated by the urine. Of the *carbon* taken into the system, a relatively larger proportion passes off by the lungs in the Horse, while a relatively larger proportion enters the urine in the Cat; this is probably because the great bulk of the carbon in the food of the Horse exists in those non-azotized compounds which can be readily converted by oxygenation into carbonic acid and water, and which consequently yield little or nothing to the urine; whilst those products of the decomposition of albuminous substances which pass into the urine, though especially rich in nitrogen, carry

with them a certain measure of carbon into that excretion. In the case of man, the researches of Pettenkofer and Voit show that with ordinary food 54 per cent. of the *water* discharged from the body is eliminated by the kidneys, 5 per cent. with the fæces, and 41 per cent. by the lungs and skin. The amount of *carbon* discharged per diem on mixed food by the skin and lungs is about 3900 grains, of which 4 per cent. is excreted by the kidneys, 6 per cent. by the bowels, and 90 per cent. by the lungs. The amount of *hydrogen gas* eliminated is small, and the major portion of this element passes away in combination with oxygen as water. The quantity of *nitrogen* varies considerably, but with sufficient mixed diet is equal to 300·6 grains daily. Parkes* finds that of this, 25 grains pass off by the bowels per diem, the remainder being eliminated by the urine. The proportion of the alvine to the total excretion of nitrogen varies from 8·1—11·45 per cent. (Parkes); according to Ranke it is 8 per cent. The amount of *Oxygen* absorbed with sufficient food is 12,845 grains, whilst during fasting it is 14,793 grains. In the fasting state more oxygen is taken up than carbonic acid is eliminated, the proportion being 106 : 100; when food is taken, on the other hand, the proportion of oxygen absorbed to carbonic acid eliminated is as 100 : 90; in the latter case the carbon is derived from the hydrocarbons or carbohydrates in the food, whilst in the former it is derived from the tissues, in which case a much larger amount of oxygen is required, the carbohydrates containing much more oxygen.

316. Thus, then, we see that, throughout life, a continuous interchange of material takes place in the very substance of the tissues, and the new material, derived from without, is being constantly laid down to replace the old and effete substance, which, in the act of developing force in one form or another, undergoes oxidation, and, as we shall hereafter see (CHAP. XI. SECT. 3), is then taken up by the circulating current to be removed by the excretory organs. In the earliest periods of life, how active soever the oxidizing processes may be, the power of the fabric to seize and apply the substances employed as food is superior, and the results are seen in the processes of growth and development. In adult life the balance is more equally preserved, and all the faculties of the body attain their highest state of efficiency. But in old age, with the increasing debility of all the vegetative processes, with diminished capability of absorption, diminished energy and rapidity of the circulating current, with more compact and drier tissues, there comes to be a gradual deficiency in the processes of nutrition, until at length the body ceases to be able to nourish itself, the waste is greater than the supply, and the death of extreme old age may be justly compared, in the wasting oftentimes preceded by the degeneration of the tissues and the gradual failure of the temperature, to death by inanition.

317. Of all the constituents of the body, none are of more complex chemical composition, and undergo more numerous and varied changes, than *Albumin*.† The relations which this substance bears to the living body are of the most important and fundamental character; since, as elsewhere shown, it enters largely into the composition of the muscles, nerves, and glandular structures, whilst it also affords the chief material for the production of the fibrin, and hæmoglobin of the Blood. It appears, however, to be itself entirely destitute of formative capacity; for in no exudation which is purely serous do we ever

* 'On the Elimination of Nitrogen from the Human Body,' "Croonian Lectures," "Lancet," vol. i. 1871.

† The formula given for it by v. Gorup-Besanez being $C_{216}H_{169}N_{27}S_3O_{68}$, and by Theile $C_{143}H_{124}N_{17}S_2O_{46}$.

trace the slightest indication of organization; and its conversion into the various kinds of tissues, therefore, must be entirely due to their own power of appropriating and transforming it after it has undergone assimilation. The great function of the Albumin of the blood, then, is to supply the material for these various transformations; and we accordingly find that whatever other changes the fluid may undergo, whether it loses its fibrin or its red corpuscles, or both, albumin is still present in abundance. Its ultimate source is to be found in the food; but the serous liquid which percolates the tissues of the body may be regarded as a reserve store, to be drawn upon in case of need, furnishing albumin to the blood when it might otherwise be deficient; and thus perhaps it is that abstinence or repeated losses of blood do not produce the degree of depression in the proportion of albumin which might be expected from the very marked reduction they effect in that of the corpuscles. When an excess of Albuminous matter is ingested as food, the injurious effects which might follow the too great augmentation of this constituent of the Blood appear to be averted by the readiness with which it undergoes *retrograde* as well as *progressive* metamorphosis; for, if not speedily subjected to the latter change, it appears in the ceaseless interchange which takes place between the contents of the cells of which the body is composed and the fluids, as the lymph and blood bathing their external surfaces, to be affected by decomposing agencies, and to be eliminated from the system by the excretory apparatus, under the form of urinary and biliary matter. From various considerations it would appear the albuminous compounds in their retrograde metamorphoses are capable of breaking up into two groups of substances, of which one contains the whole of the nitrogen, whilst the other is composed of carbon, hydrogen, and oxygen alone. The former are ultimately eliminated from the body as urea or some analogous compound; the latter are either stored up in the form of fat or are discharged after oxygenation in the form of carbonic acid and water. Of the former series, we know that whilst Leucin ($C_6H_{13}NO_2$), Tyrosin ($C_9H_{11}NO_3$), and Glycin ($C_2H_5NO_2$), can be artificially formed by the action of alkalies or acids upon albumin, or even appear during its spontaneous decomposition; these same substances can also be obtained from various tissues of the body, and are always most abundant in those organs in which interstitial changes are most active, as in the spleen and liver.* From muscular tissue, again, Inosinic Acid ($C_{10}H_{14}N_4O_{11}$), Creatin ($C_4H_9N_3O_2$), and the urinary constituent Creatinin ($C_4H_7N_3O_1$), can be directly obtained. The relation of Inosinic Acid and of Allantoin ($C_4H_6N_4O_3$), found in the urine of women during gestation, and in new-born children, to Uric Acid and Urea, which are the ultimate products of the decomposition of the albuminous compounds, is very intimate; whilst, as regards Creatin, the researches of Sarokow† indicate that during active muscular exertion it is converted into Creatinin, or at all events that, in muscles exhausted by action, a greatly increased proportion of Creatinin is generated; and it is well known that both of them are convertible by chemical agents into Urea.‡ The evidence of the derivation of the fatty compounds from the albuminous substances will be given in the next section, and, like that indicating the origin of the farinaceous and saccharine compounds from them, is chiefly of an indirect nature. In regard to the analogous compound, glycogen, it may be observed that the formation of an amyloid substance is the natural function of the liver, and

* Glycin has not, indeed, been obtained in the separate state, but it enters into the composition of the glycocholic acid of the bile. The further decomposition of leucin in the laboratory by fermentation and oxidizing agents, yields the volatile fatty acids well known to occur in glandular organs and in the blood.

† Virchow's "Archiv," 1863, p. 544.

‡ Fownes' "Chemistry," 1861, p. 670.

there is some reason for believing that this is an intermediate stage of the decomposition of albumin into fat; the formation of the glycogen being accompanied by the simultaneous appearance of highly nitrogenous substances, such as Glycocholic and Taurocholic acids, which have been shown by Liebig to be readily derivable from albumin, the latter containing an important element of albumen, namely, Sulphur. In regard to the albuminous, and, as the experiments of Bischoff and Voit appear to prove, the gelatinous constituents of our food also, it is probable that by far the largest part is applied directly to the formation of tissue, including under this term the contents of gland-cells, whilst a much smaller portion, if indeed there be any, termed the "Luxus consumption" by the Germans, is decomposed in the blood without forming tissue. In both instances a kind of decomposition or disintegration takes place under the influence of oxygen, by which, on the one hand, such compounds as Fibrin, Chondrin, Keratin, Taurin, Glycin, Leucin, Creatin, Creatinin, Guanin, Sarkin, Xanthin, Uric Acid, Urea, &c., are formed, which are, for the most part, discharged by the Urine and Fæces; and on the other, certain fatty or saccharine substances are generated, by the further combustion of which the animal heat is maintained, their ultimate products, consisting of Carbonic Acid and Water, being eliminated chiefly by the skin and lungs.

318. As regards the *fatty constituents* of the body, a large proportion is doubtless derived from the oleaginous compounds consumed in the food, though it is certain that a part may also proceed from the metamorphosis or disintegration of both hydrocarbonaceous and albuminous compounds. Of the fats ingested, a portion, after reduction to the fluid state and minute division, is directly absorbed, whilst a smaller portion appears to be decomposed by the pancreatic juice into the fatty acids and glycerin before absorption. It has been suggested by v. Gorup-Besanez that the fat directly absorbed would, under the influence of the active oxygen and alkaline carbonates of the blood, also soon undergo decomposition into the fatty acids and glycerin, which again, by further oxidation, give rise to formic, propionic, and other acids.* It seems reasonable to suppose that the stearates, oleates, and margarates are directly applied to the formation of adipose tissue.† But that the adipose tissue of an animal does not proceed exclusively from the fats ingested with the food is conclusively shown by the experiments of Lawes and Gilbert,‡ who found that in fattening pigs, for every 100 parts of fat in the food, 400–500 parts of fat were stored up in the body of the animal. The question then arises, Does the excess of fat laid down in the body over the fat ingested proceed from the hydrocarbonaceous or from the albuminous constituents of the food? The experiments of Liebig§ and others upon Bees, showing that if these animals be fed upon pure sugar they are yet able to furnish wax for the comb, and the observations of Boussingault, Lehmann, Groner, and Lawes and Gilbert on ducks, geese, pigs, and oxen, showing that on a diet rich in carbohydrates fat is abundantly formed, and either deposited in the tissues or excreted in the milk or fæces, coupled with the well-known fact that negroes rapidly fatten during the period of cutting the sugar-canes, lead to the conclusion that the

* Schulz, Pflüger's "Archiv," Band xv. 1877, p. 403, has shown that at ordinary temperatures, oxygen, even when pure, has no action on fats; the first traces of carbonic acid gas appear at a temperature of 116° C.

† See Hofmann ("Zeits. f. Biologie," Band viii. p. 153). Radziejewski (Virchow's "Archiv," Band x. liii.) and Subbotin ("Centralblatt," 1870, p. 675) are however opposed to this view, because they found, that, although when certain fats with well-marked chemical properties, as spermaceti, were introduced into the alimentary canal of a dog, they underwent absorption, yet they could not be subsequently detected in the subcutaneous fat.

‡ "Philosoph. Transact.," 1859, p. 543. See also Pettenkofer and Voit, "Zeitschrift f. Biologie," Band ix.

§ Gundlach, Huber, Dumas, and Milne-Edwards.

fat of the body may be derived from the carbohydrates, and this is supported by the observation of Pasteur, that in the alcoholic fermentation of sugar Glycerin is one of the products. Lawes and Gilbert estimate that 2½ parts of starch must be consumed in the food to produce one part of fat, the proportion of sugar required being somewhat larger.* But evidence has also accumulated, showing that the fat of the body may be derived from the albuminous compounds; thus Pettenkofer and Voit found that on very full or excessive meat diet their dog excreted considerably less carbon than he ingested, though the quantities of nitrogen ingested and egested were almost exactly equal, and as the animal gained in weight and fat was deposited in its tissues, there was strong reason for believing that it was due to the separation of a part of the albuminous compounds in the form of fat. Other facts which may be mentioned as tending to prove the same thing are the production of adipocere from muscle: the observations of Blondeau, Hoppe, Kemmerich, and Fleischer, that fat can be deposited during a diet composed mainly of cheese; the formation of fat during the maturing of cheese; and the development of fat in a fasting dog when the animal is slowly poisoned with phosphorus; the experiments of Subbotin showing that bitches secrete milk containing the largest amount of fat when the food has been abundant, though composed essentially of lean meat; the observations of Burdach† upon the eggs of Lymnæus, one of the water snails, showing that in the progress of incubation the fat increases apparently at the expense of the albumen, so that whereas in the early stage the amount of fat is about 7 per 1000 and of albumen about 9·53, in the last stage the amount of fat has increased to about 22 parts, whilst the albumen has fallen to 9·18 in 1000 parts; and lastly, the recent experiments of Pettenkofer and Voit‡ all afford strong support to the view that the fats may be derived from the albuminous compounds, the observations of these investigators appearing to demonstrate that when a sufficient amount of albuminous food is supplied, fat ingested as such is stored up in the body, the carbohydrates burnt to maintain the animal heat being really derived from the disintegration of the albumin, which they estimate yields about 55 per cent. of its weight of fat. The phenomena presented in nerve-cells and muscular tissue during the pathological process of fatty degeneration may also be referred to as supplying additional evidence.—The Fatty matters of the Blood, besides being destined to furnish the contents of the Adipose and Nervous vesicles, appear also to be required in the early stages of the production of cells generally. The principal source of their expenditure, however, is that process of combustion by which the heat of the body is maintained; and the amount deposited in the tissues as fat may be looked upon as the surplus of the quantity ingested that is not thus consumed. The quantity of fatty matter in the blood is liable to sudden augmentation from the introduction of a large quantity furnished at once by the alimentary material; and this excess will continue until the surplus has been eliminated, either by the combustive, the nutritive, or the excretory operations. These last do not ordinarily remove the saponifiable fats from the body; for although the mammary secretion in the female draws off from her blood a large quantity of fatty matter, this is destined, not for its purification, but for the nutrition of her offspring; and cholesterin appears to be the only

* The opponents of the view above given, that fat may be derived from the Carbohydrates, contend that the purely chemical evidence is weak, since only fatty acids, poor in carbon, and *traces* of Glycerin and Glycerides, make their appearance in saccharine fermentations.

† F. W. Burdach, 'De Commut. Subst. Prot. in Adipem "Dissert.," 1853.

‡ "Zeits. f. Biologie," Band ix. Heft 1. Weiske und Wildt, "Zeits. f. Biologie," Band x. 1874, p. 1.

fatty substance which is normally excreted for the purpose of being removed from the body. The quantity of fat contained in different parts of the body varies considerably, but it is almost universally present. The blood usually contains about 0·4 per cent., the muscles 3·3, milk 4·3, brain 8, the nerves 22, and adipose tissue 83 per cent. The ultimate disposal of the *saccharine constituents* of the body, which appear to be partly derived from without, and to be partly the result of the decomposition of the albuminous constituents of the blood, as will be hereafter more fully considered (Glycogeny), is still unknown; though there seems to be some probability in favour of their being first converted into Lactic acid, and finally into Carbonic acid and Water, and as these are more easily oxidized than the fats, they spare the latter from combustion.

319. The uses of the various Inorganic compounds, which, as being uniformly present in the Blood, must be considered among its integral constituents, have already been pointed out (§ 58), and it need only here be remarked that the observations of Weiske* show that the bones retain their hold of the salts that enter into their composition with great tenacity, so that if food be supplied in which the proper salts are defective, no material difference can be detected for a considerable period in the composition of the osseous tissue. Papillon† has demonstrated that the Bones contain a large proportion of strontium phosphate, or of magnesian phosphate, replacing the calcium phosphate, if these salts are liberally given with the food, and providing the calcium phosphate is deficient or altogether absent.

320. We may now proceed briefly to consider what is the amount and nature of the work done in and by the body, and endeavour to ascertain the mode in which the food consumed is applied to the production of that work. It has already been stated that the two principal circumstances occasioning a demand for alimentary material are the supply of the loss caused by the activity of the nervo-muscular apparatus, and the production of the heat requisite to maintain the body at a uniform standard. The actual disintegration of the material substratum of the nervous and muscular tissues during exertion appears to be exceedingly small, since fasting animals, or animals fed on non-nitrogenous diet, can for a considerable period perform severe work without the occurrence of any considerable increase upon the amount of nitrogenous excreta eliminated by the same animals when at rest with the same diet. Yet that the tissues really undergo disintegration during exertion, and that they require appropriate nitrogenous food for the repair of the loss occasioned by their wear and tear, is clearly shown by their incapacity for performing work except for a limited period without such supplies. It is reasonable then to suppose that, whilst a certain small portion of the large store of albuminous and other nutritive material present in the body is applied to the nutrition and repair of the work-performing tissues, a very much larger proportion is applied to the development of the forces of various kinds which are exerted by them. The three principal classes of food—the albuminous, farinaceous, and oleaginous—are all of them composed of easily oxidizable material, and it is conceivable that in the act of combining with oxygen, or rather with ozone, the force may either become directly apparent as heat or electricity, or may, through the agency of muscle-, gland-, or nerve-tissue produce movement, secretion, or thought. We have only indirect means of estimating this last; but the quantity of food required for the mechanical and

* "Zeitschrift für Biologie," vii. pp. 179 and 333.

† "Journal de l'Anatomie," 1873, No. 3; see also, König, "Zeits. f. Biologie," Band x. 1874, p. 68. The statement is contested by Weiske, *ibid.* 1872, Band viii. p. 239.

calorific force developed by the body has been rendered capable of being estimated by the experiments of Frankland, Haughton, and others.

321. According to the observations of Professor Frankland, one gramme (15·44 grains) of purified albumen, when burnt in oxygen, yields 4·998 units of heat. Now each unit of heat can be converted into mechanical force, expressed in kilogrammeters, by multiplying it by the number 423; that is to say, the heat required to raise one kilogramme of water 1° C. if converted into mechanical force would raise 423 kilogrammes one meter in height, or an amount of heat equivalent to 1° C. would be produced by the expenditure of an amount of force equal to the raising of 423 kilogrammes to the height of one meter; hence one gramme of albumen burning in oxygen yields 4·998 + 423 or 2117 kilogrammeters—that is, a force sufficient to raise 2117 kilogrammes to the height of one meter. But it is to be remembered that albumen, in passing through the body, is not so completely oxidized as when burnt in oxygen. It is only reduced to the condition of urea; and Professor Frankland has shown that urea can itself be burnt in oxygen, yielding 2·206 units of heat, which is equal to 934 kilogrammeters of force; and as it is found that one gramme of pure albumen in passing through the body furnishes almost exactly one-third of its weight of urea, the effective force developed in the body by its consumption is obviously less than when it is burnt in oxygen to the extent of the amount of force still produced when one-third of a gramme of urea is burnt in oxygen. Hence the effective force of one gramme of albumen is equivalent to 1803 kilogrammeters.* Fat, on the other hand, is as completely burnt in the body as outside of it, and yields, weight for weight, a much larger amount of effective force than albumin. The following Table contains some of the more important determinations made by Professor Frankland:—

Name of the Food.	Effective energy when one gramme of the different substances named is burnt in Oxygen.					Effective energy when consumed in the body in kilogrammeters.	
	Units of Heat.		Kilogrammeters of Force.		Per-centage of water.	Dry.	Natural state.
	Dry.	Natural state.	Dry.	Natural state.			
Albumen	4·896	671	2074	284	86·3	1781	244
Lean Beef	5·313	1567	2250	664	70·5	2047	604
Fish (Mackerel)	6·064	1789	2568	758	70·5	2315	683
Fat of Beef	9·069	—	3841	—	—	3841	—
Starch	—	3941	—	1669	—	—	1627
Sugar (white)	—	3348	—	1418	—	—	1418
Gelatin	4·520	—	1014	—	—	1550	—
Bass's Ale, including the alcohol	3·776	775	1559	328	88·4	—	—

322. The amount of work done by the body may be divided into—1. Calorific work; 2. Internal mechanical work, such as is required for the main-

* It must be acknowledged that the estimates of different experimenters in regard to the calorific value of different substances vary considerably. Thus, Franke estimates that the combustion of one gramme of starch produces 5232 units of heat, Ludwig 4568, Dulong 3232, Bischoff and Voit 5100, and Frankland 3941. The warming of one pound of water 1° C. is equivalent to a mechanical force of 1390 foot-pounds.

tenance of the circulation, respiration, digestion, &c.; 3. External mechanical work, expended in the movements of locomotion, lifting and carrying weights, &c.; 4. Mental work. And lastly, in youth, the work of growth. The absolute amount of *heat units* daily produced by an adult of average weight has been estimated by Ranke at 2200 (by Helmholtz at 2700), or sufficient to raise the temperature of 48·4 lbs. from the freezing to the boiling point;* or if converted into mechanical force, it amounts to 930,600 kilogrammeters, which would be sufficient to raise the body of a man weighing 68 kilogrammes (149·6 lbs. av.) through a vertical height of 8·5 miles. This heat is expended in conduction and radiation from the body, in warming the air inhaled, and the water and watery vapour exhaled by the skin, kidneys, and lungs, and in warming the food. Next as regards *internal dynamical* work. Professor Haughton† states that the work done in maintaining the circulation and respiration may be estimated at 133 foot-tons, or 41,180 kilogrammeters (heart = 121 foot-tons, muscles of respiration = 11 foot-tons). The same authority gives as the result of numerous observations on the *external* or daily work of various classes of labourers the mean of 353·75 foot-tons (109,549 kilogrammeters), which corresponds well with the results obtained by Coulomb (330 foot-tons), Lamandé (352 foot-tons), and Playfair (346 foot-tons). The work expended in *growth* may be neglected for the adult; and that exerted in *mental operations*, as already stated, can only be indirectly estimated. From the foregoing calculation it would seem that the entire amount of force expended in maintaining the heat of the body of an adult weighing 150 lbs., and in the performance of his internal and external mechanical work, is 1,044,267 kilogrammeters, of which nine-tenths is expended in maintaining the heat, and the remainder in external and internal dynamical work.‡

323. It may be shown, either from an examination of Frankland's Tables, or by calculating the amount of tissue decomposed to furnish the usual amount of urea, carbonic acid, and water eliminated from the body, that almost exactly the same amount of a million kilogrammeters of force are contained in the food. Thus, on Vierordt's estimate—

120	grammes of albumen, dry	= 213,720	kilogrammeters.
90	„ of fat	= 345,690	„
330	„ of farinaceous compounds . . .	= 536,910	„
		1,096,320	

Or on Voit's estimate§ of 118 grammes of albumin, 56 grammes of fat, and 500 grammes of carbohydrates, we have a rather larger number—

118	grammes of albumin	210,150
50	„ of fat	192,050
500	„ of carbohydrates	894,865
		1,297,065

The close approximation of the experimental with the calculated values is of great interest. It may be objected that a very small margin is left for purely mental operations; but it must be remembered that Professor Haughton's

* "Grundzüge der Physiologie," p. 476, 1868.

† Haughton, Address, delivered at the British Medical Association at Oxford, Aug. 1868. Dr. Andrew Buchanan gives reasons for believing that the force of the heart (Left Ventricle) does not exceed 42·3 foot-tons in the 24 hours. See "Lancet," vol. ii. 1870, p. 665.

‡ Professor Haughton, calculating the amount of heat produced from the amount of Carbonic Acid gas eliminated, as shown in Ranke's experiments, estimates the calorific work at five-sixths, and the internal and external mechanical work at one-sixth of the whole amount of force generated.

§ "Untersuchungen der Kost in einig. öffent Anstalten," 1877.

estimate of 353·75 foot-tons, or 109,549 kilogrammeters, for external or mechanical work is very high, being equivalent to that required to raise the body through one mile of vertical height, or to walking 20·74 miles per diem, which is perhaps three times more than is usually accomplished; and that, under such circumstances, either little mental work would be done, or more food would be required. Supposing only seven miles were walked, 118 foot-tons of force would be required, leaving 236 foot-tons available for mental work; but it must be remembered that both mental work and much of the internal mechanical work are again expended in the body. A part of the mechanical force exerted by the heart is given up as heat from obstructed motion in the capillaries, and will be included in the heat given off from the body; and, although nothing positive can be stated as to the form taken by mental work and nervous action generally, it is highly probable that for the most part this is heat. There is every reason to believe that, although the tissue of the nerves and muscles cannot be built up from alimentary materials destitute of nitrogen, the force which can be exerted by those tissues proceeds both from the disintegration and oxidation of nitrogenous as well as non-nitrogenous substances. At any rate, it has been clearly shown by Professor Haughton that the amount of urea (501 grains) eliminated after severe exercise does not represent the oxidation of a sufficient amount of nitrogenous material to account for the work done; nor is there any remarkable increase in the excretion of urea after severe bodily exertion. Moreover, whilst in carnivorous animals the force must proceed from the oxidation of nitrogenous constituents, since they can be nourished upon lean flesh, in herbivorous animals—and, as Verloren has pointed out, in mature insects, as bees and butterflies—it seems equally evident that the nervo-muscular force is generated from the oxidation of farinaceous compounds; and an examination of the excreta gives additional testimony to the same effect. Thus, Professor Haughton found the daily elimination of urea in a Bengal tiger to be 4375 grains, whilst in a sheep it was only 256 grains. It has also been shown by the same observer that in diabetes, where sugar is eliminated by the urine, instead of undergoing combustion, and being discharged from the body in the form of carbonic acid and water, an increased quantity of food is required, which is accompanied by an increased discharge of urea, showing that the nitrogenous materials are consumed to maintain the temperature and to furnish the force required for work, which is always small. Heaton suggests that the whole, or nearly the whole, of the force of the body is generated in the blood, and that Mayer was perfectly right in saying that the muscle produces mechanical effect at the expense of the chemical action occurring in its capillary vessels. It is probable, however, that the oxidising processes take place essentially in the tissues and intertextural fluids.

324. Of the mode in which the substitution of new tissue for that which has become effete is effected in the process of Nutrition, our knowledge is at present limited; but there can be little doubt that it nearly always takes place in a manner closely conformable to the first development of each tissue. In some instances there is an obvious *replacement* of the old and dead by the young and active elements; this is the case, for example, in the constantly-repeated production of the Epidermic and Epithelial layers; for whether they are developed from germs embedded in the subjacent basement-membrane, or from nuclei formed *de novo* in the blastema on its free surface, or by the duplicative subdivision of pre-existing cells, there is a continual succession of new cells, which takes the place of those that are cast off as defunct and useless. So in the growth of Hair, the increase of which takes places only at its base,

re can trace at any period the same development of newly-formed spheroidal ells into horny fusiform fibres, as that which occurred when first the hair egan to sprout from the aggregation of epidermic cells at the bottom of its ollicle. So, again, in the vesicular tissue which constitutes the essential part f the Nervous centres, there are appearances which indicate that its peculiar ells are in a state of continual development, newly-formed ganglionic vesicles aking the place of those which have undergone disintegration. But there re other textures, whose nutrition is more completely *interstitial;* their lements being more closely coherent, and their newly-formed portions being eveloped throughout the substance of the old, instead of (as in the case of the pidermis and its appendages) *superficially* or in mere continuity with it. uch is the case, for example, with Muscle, the mode of whose nutrition has ot yet been elucidated. We can only infer from analogy, that here too each ibre or fibril will pass, in the course of its development, through the same tages which those of the embryo did when its muscles were first formed. And his analogy seems to derive support from the presence, in all well-nourished nuscles, of nuclei; for these, as Sir J. Paget remarks, "are not the loitering mpotent remains of embryonic tissue, but germs or organs of power for new ormation." And it is further confirmatory of this view, that losses of ubstance of muscle which involve the destruction of these centres of nutrition re not replaced, like losses of cuticle, by new tissue of the same kind; the ower to form it not being inherent in the blood or in the neighbouring parts. Nevertheless it must be admitted that no intermediate stages of development can be traced in the fibres, even of those muscles of the adult which are in most constant use, and of which the nutrition is the most active, that are at all comparable to those which are met with in the muscular tissues of the embryo. —With regard, again, to the interstitial nutrition of Bones and Teeth, we have no certain knowledge. That some movement of nutritive fluid is continually taking place through them, is made apparent by the effects of madder in gradually tinging even the bones and teeth of the adult, though for such a change a much longer period is required in the adult than in the young animal; how far this movement, however, is subservient to any continual change of substance, still remains doubtful. If the supply of blood be withdrawn from a tooth or from a bone, or even from a part of the latter, the structures thus cut off from connection with the act of nutrition soon die, become detached from the living parts around, and are thrown out of the body. Of this we have a very good example in the annual exuviation of the antlers of the Deer, which is partly brought about by the choking up of the Haversian canals that give passage to blood-vessels, with concentric osseous deposit, and partly, as Lovén,* Kölliker,† Morison,‡ and others have shown, by the absorptive power of peculiar, multi-nucleated giant cells (the Myeloplasts or Osteoclasts of Robin, and Riesenzellen or giant cells of Virchow). Something of this kind seems to be continually taking place in ordinary Bone, upon a more limited scale; individual Haversian systems being removed by absorption, leaving spaces termed the Lacunæ of Howship, and being replaced by new formations of the same kind, probably during its whole life, without any change in external configuration. So far as can be gathered from observation, the process of interstitial decline and death usually takes place too rapidly for its stages to be perceptible, and is *immediately* followed, in the normal condition

* Lovén, "Wurzburg Phys. Med. Verhand." N. F., 1873, Band iv. p. 1.

† Kölliker, *idem.* p. 34. See the Memoir by Messrs. Tomes and De Morgan 'On the Structure and Development of Bone' in "Philos. Transact.," 1853, p. 111.

‡ "Edinb. Med. Journ.," Oct. 1873.

of the system, by the removal of the effete particles; so that it is only when this removal is from any cause obstructed, as happens in the cases to be presently cited, that we see any indication of the *stages* through which the disintegrating tissues pass.

325. There is one remarkable form of degeneration, however, which is common to nearly all the tissues, and which seems to occur as a normal alteration in many of them at an advanced period of life; this consists in the conversion of their albuminous or gelatinous materials into fat, thus constituting what is known as *fatty degeneration*. That this change is not due to the removal of the normal components of the tissues, and the substitution of newly-deposited fatty matter in their place, but is (in most cases at least) the result of a real conversion of the one class of substances into the other, may now be considered as well ascertained.* And there are certain facts which indicate that this kind of degeneration is a part of the regular series of processes by which tissues that have served their purpose in the economy are prepared for being removed by absorption; one of the most remarkable being the observations of Virchow† and Kilian‡ with regard to the fatty degeneration of the muscular tissue of the uterus after parturition, and quite analogous phenomena are observed in muscles the motor nerves of which have been divided.§ So, as Sir J. Paget has pointed out, the fibrinous and corpuscular products of inflammation are often brought into a state fit for absorption, by passing through this intermediate stage; the fibrinous substance being observed to be dotted by granules which are recognized as oil-particles by their peculiar shining black-edged appearance, and at the same time losing its toughness and elasticity, and being no longer rendered transparent by acetic acid; whilst the lymph-cells present a similar increase of shining black-edged particles like minute oil-drops, which accumulate until they nearly fill the cell-cavity, their nuclei at the same time gradually fading and disappearing.‖ Thus, then, if the fat, which is one of the products of this retrograde metamorphosis, be absorbed as fast as it is formed, and the effete tissue be replaced by a new production (as seems to be the case with Muscles in a state of healthy activity), there is no appearance of degeneration, and the nutrition is kept up to its normal standard. So if, from the advance of age, or from the insufficient exercise of the muscles, their nutrition takes place less rapidly than their waste, whilst the products of their degeneration are still removed, simple atrophy is the result. If, on the other hand, the general conditions being similar, the fat produced in degeneration be not absorbed, but remain in the tissue, an obvious "fatty degeneration" is the result. This seems most likely to happen either when the fat is thus produced in such excessive amount, that the ordinary rate of its absorption (corresponding with that of its elimination by the combustive process) does not provide for its removal; which will occur when a large amount of tissue is undergoing degeneration at once, as in the case of the uterus after parturition: —or when the blood, being already highly charged with respiratory material,

* For an excellent account of the whole subject of Fatty Degeneration, see Dr. Handfield Jones's Articles in the "Brit. and For. Med.-Chir. Rev.," vol. xi. p. 327, and vol. xii. p. 30. In this country, a substantial description of the importance of the fatty degenerations was given, upwards of a quarter of a century ago, by Gulliver ("Trans. Med.-Chir. Soc.," 1843, vol. xxvi., and "Edinb. Med. and Surg. Journ.," July, 1843, p. 158), who thus early proved that these degenerations are a most frequent cause of the decay of the tissues, especially of aneurism of the arteries, and of that spontaneous bursting of their small branches which is the proximate cause of the most frequent form of apoplexy in the brain.

† "Verhandlungen der Gesellschaft für Geburtshülfe," Berlin, vol. iii. p. 17.

‡ Henle and Pfeuffer's "Zeitschrift," vol. ix. p. 1.

§ See Erb, "Centralblatt," 1868, p. 115; Bizzozero and Golgi, Stricker's "Jahrbücher," 1873, p. 125.

‖ See Sir James Paget's "Lectures on Surgical Pathology," vol. i. p. 374.

s indisposed to receive an additional amount of fat.* This distinct evidence of the operation of Alcohol habitually received into the blood in large quantities, affords an obvious indication that the habitual consumption of even a much smaller amount will tend to produce fatty degeneration at more remote periods and in a less aggravated degree; and the participation which this state has been shown to have in the production of a large proportion of the diseases of Old Age,—especially by the changes it induces in the texture of the heart and of the walls of the blood-vessels (which are particularly liable to it),—fully bears out this idea.

326. It may be stated as a general rule, that no absorption of the materials of tissues can take place without a previous degeneration such as this, or a more complete decomposition. There is no evidence that any *healthy* tissue is ever thus absorbed, or that any preternatural activity of the absorbent vessels can ever (as formerly supposed) be the *occasion* of a loss of substance; in fact, so long as the vital force is in active operation in a part, and its processes of growth and development are being normally carried on, such absorption may be considered to be impossible. On the other hand, if a part die *en masse*, it is not removed by absorption, but becomes isolated by the separation and recedence of the living parts, and is then cast out altogether, even from the interior of the body, as we see in the case of a necrosed bone; its condition being then essentially the same as that of the outer layers of the tegumentary organs, which are cut off, by their distance from a vascular surface, from all further nutrient change. The difference between these two modes of removal is well seen (as Sir J. Paget has remarked) in the case of the Teeth; for the fangs of the deciduous teeth undergo degeneration when the current of nutrition is diverted towards those which are to suceeed them, their materials being slowly decomposed, so as to become soluble, and being gradually removed by absorption, so that nothing is left at last but the crowns of the teeth; on the other hand, the permanent teeth, which are not to be succeeded by others, when no longer receiving their due nutrition, die, and are cast out entire.

327. Among the conditions of healthy Nutrition, a due supply of Nervous power is commonly enumerated; and it cannot be questioned that the want of such a supply is frequently the source of a perversion of the normal operations. This, however, by no means proves that the formative power is derived from the nervous system; and such an idea is at once negatived by a number of incontestable facts. Yet it may be freely admitted that the right direction and application of this power in nutrition may sometimes depend upon guidance and direction afforded by the Nervous centres, in the same manner as the Secreting process is capable of being thus affected; in fact, we can scarcely explain in any other mode that influence of mental states upon the nutrient operations which frequently leads to very important modifications of them. —The whole of this subject, however, will be more appropriately considered hereafter (CHAP. XVII.).†

* The quantity of fat in the blood of drunkards has been found in some cases to be as much as 11·7 parts in 1000 (Lecanu), the highest estimate of the quantity in health being 8·65 parts. Scharlau has found as much as 30 per cent. more carbon in the blood of a drunkard than in that of a healthy man.—See Dr. Huss's treatise on "Alcoholismus Chronicus," Rokitansky's "Handbuch der allgemeinen pathologischen Anatomie," Band iv., and "Brit. and For. Med.-Chir. Rev.," vol. xii. pp. 33, 34.

† In the treatment of this subject, the Author has made use of valuable illustrations contained in the first three of Sir J. Paget's "Lectures on Surgical Pathology;" the general doctrines, however, being such as he had himself expressed on many previous occasions.

3. *Varying Activity of the Nutritive Processes.—Reparative Operations.*

328. Without any change in the *character* of the Nutritive processes, there may be considerable variations in their *degree of activity;* and this, as regards either the entire organism or individual parts, though most commonly the latter. These variations may be so considerable as to constitute Disease; though there are some which take place as part of the regular series of Physiological phenomena. Thus, as we have seen, it is to the excess of formative activity that the increase of the organism in the earlier period of life is due, its 'waste' being at the same time extremely rapid; whilst it is to a corresponding reduction in the regenerative power, and not to positive excess of 'waste' or decay (this, indeed, taking place very slowly), that the gradual decline of the organism in advancing years is to be attributed. So also we find that local as well as general variations may take place, as a part of the regular series of vital phenomena; and this during the period of adult life, as well as in the earlier and later epochs. Thus all those differences in the proportional development of the several parts of the organism which mark the distinction between the adult and the child, even where (as in the case of a dwarf) there is no difference in stature, result from a decline in the formative capacity of those which are peculiarly adapted to the wants of the earlier stage (the Thymus Gland, for example), and from an increased activity of nutrition in those which are destined to the use of the adult, the Generative organs more particularly. And the intermittent activity of the sexual apparatus of the female affords a remarkable example of the same principle; this being marked, not merely in the enormous development of the uterus and mammary glands as a consequence of conception, but in the periodical change which takes place in the ovaries, whereby the ova are matured and thrown off at certain regular intervals. The decline in the formative power of these same organs, moreover, when as yet the organism in general shows but little indication of deterioration, is another characteristic example of the variation in Nutritive activity resulting from the inherent endowments of the part, and essentially irrespective of the condition of the blood, of the circulation, and of the organism as a whole; although, as formerly shown, the production and maintenance of other and apparently unconnected organs are *complementally* dependent upon the formative activity of the Generative apparatus.

329. The abnormal excess of Nutritive change which properly constitutes *Hypertrophy*, appears to depend upon a departure from one or other of the conditions under which, as already specified, the change normally takes place —namely, the right composition of the blood, a due supply of such blood, and a proper formative capacity in the blood itself.—Of the excess of nutrition resulting from the presence of an excess of the peculiar materials of certain tissues in the circulating fluid, examples have already been given. It is important to remark, however, that although hypertrophy may be thus induced in any of the tissues which constitute the instruments of *organic* life, yet there is no evidence that either the Nervous or the Muscular apparatus can be forced (so to speak) to an augmentation in bulk by the mere abundance of their nutritive materials.—With regard, in the next place, to the supply of blood, there can be no doubt that in general an increased flow of blood towards a part is consequent upon, rather than a cause of, an excess in its nutritive activity; but still there are cases in which its causative agency may be traced. Various examples of this have been supplied by the experiments and observa-

tions of John Hunter, the records of which are left in his Museum. Thus, if the spur of a cock be transplanted from the leg to the comb, which is a part far more vascular than that with which it was originally connected, it undergoes an extraordinary augmentation in size; having in one instance grown in a spiral form, until it was six inches long; and in another, curved forwards and downwards like a horn, so that its end needed to be often cut, to enable the bird to bring its beak to the ground in feeding. So, again, it was remarked by Hunter, and has been frequently observed since, that an increased growth of hair often takes place on surfaces to which there is an increased determination of blood as a consequence of inflammation in some neighbouring part, though not from the surface of the inflamed part itself. So it sometimes happens, that when an ulcer of the integuments of the leg has long existed in a young person, the subjacent bone may share in the increased afflux of blood, and may enlarge and elongate. And it seems not improbable that we are to attribute the increased thickness of the cuticle, on parts which are exposed to continual pressure or friction, to the augmented afflux of blood which is determined to the irritated surface.*

330. The greater number of cases of hypertrophy, however, must undoubtedly be referred to the preternatural formative capacity of the part itself, and this may either be congenital or acquired. Of this congenital excess, we have a remarkable example in the abnormal growth of an entire limb, or of fingers or toes,† which cannot with any probability be referred to an original excess in the supply of blood, the enlargement of the arteries leading towards such parts being almost certainly consequent upon their unusually rapid growth, just as in the case of the uterine and mammary arteries of the pregnant female. The most remarkable instances of the acquirement of increased formative activity are presented to us in that augmented growth of the nervous and muscular tissues, which is consequent upon the exercise of their functional powers. This may be considered as, to a certain extent, a normal adjustment of the supply to the demand; but there are some instances in which it takes place to such an extent as to become a positive disease. Thus it not unfrequently happens that if young persons who naturally show precocity of intellect are encouraged rather than checked in the use of the brain, the increased nutrition of the organ (which grows faster than its bony case) occasions pressure upon its vessels; it becomes indurated and inactive, and fatuity and coma may supervene. Now, although in such cases there may probably have been some congenital tendency to preternatural activity of the brain, which manifested itself in the precocity of intellect, yet there is no doubt that this may be augmented by the 'forcing system' of education; whilst, on the other hand, it may be controlled by a system of management adapted to the peculiar circumstances of the case. Excess of muscular development is peculiarly prone to show itself in the involuntary muscles; but this production is in almost every instance the result of the demand for increased muscular exertion which is consequent upon some obstruction to the usual function of the part. Thus an extraordinary hypertrophy of the muscular coat of the urinary bladder is often seen as a consequence of obstruction to the exit of the urine, through the presence of a stone in the bladder or of a stricture in the urethra. So,

* It is commonly said that local Hypertrophy may be induced by long-continued Congestion; but this is not true hypertrophy; for the bulk of the organ is not augmented by the increased production of its normal tissue, but by the addition of tissue of an inferior type of organization, as in Inflammation.

† A case of hypertrophy of an entire limb was described by Dr. John Reid in the "Edinb. Monthly Journ.," 1843, p. 198; and several cases of hypertrophy of the fingers were described by Mr. Curling in the "Med.-Chir. Trans.," vol. xxviii.

again, hypertrophy of the muscular coat of the gall-bladder may take place as a consequence of obstruction of its duct by a gall-stone. Hypertrophy of the muscular coat of any part of the alimentary canal may be induced by the existence of stricture lower down; and even hypertrophy of the heart is generally, if not always, attributable to obstruction to the exit of the blood which it propels, resulting either from stagnation of the pulmonary circulation by the deficient aëration consequent upon disease of the lungs (in which case the hypertrophy is limited to the right side of the heart), or from thickening or induration of the semilunar valves, or from narrowing of the orifices of the aorta and pulmonary artery. It is curious, moreover, to observe, that hypertrophy of muscles frequently becomes a source of increased nutrition of the bones to which they are attached; this being manifested, not merely in the augmented bulk of the bones of limbs that are specially exercised, but also in the increased prominence in the ridges and processes to which the muscles are attached. This adaptiveness on the part of the formative activity of the osseous tissue is curiously manifested also in the relation of the skull to the brain; for if the bulk of the brain be not too rapidly augmented, the skull will enlarge accordingly, and this (in some instances) not merely by the extension of its normal bones, but by the intercalation of new osseous elements, the 'ossa wormiana;' whilst, on the other hand, if there be a diminution in the bulk of the brain, the cranium may adapt itself to this also, by a thickening on its internal surface (or concentric hypertrophy),—this change, rather than a diminution in the entire substance of the skull, being more liable to take place in cases in which the cranial sutures have already closed, and the nutrition of the bone has become inactive.

331. The state of *Atrophy* is in all respects the very opposite of that of Hypertrophy; consisting in such a reduction in the rate of formative activity of the parts, as compared with that of their 'waste,' that their nutrition is no longer maintained at its previous standard; so that they are gradually reduced in bulk, or degenerate into some inferior histological type, or (which is more common) undergo both diminution and deterioration at the same time. It is important to bear in mind that Atrophy may take place, either locally or generally, from an unusually rapid disintegration of the tissues, uncompensated by a corresponding increase in the rate of their nutrition: of such local atrophy, we have a characteristic example in the rapid reduction of the bulk of the uterus after parturition, and of the mammary glands after the sudden cessation of lactation; of the general, we see an illustration in that rapid wasting of the system, which takes place in the irritable state that results from excessive and prolonged exertion of body or anxiety of mind, especially when accompanied with want of sleep, the increased disintegration being marked by the presence of an unusual amount of urea and of the alkaline phosphates in the urine. But in the ordinary forms of Atrophy, there is not merely a *relative* but an *absolute* reduction in the rate of the formative process, or a lowering of its standard of perfection; and here also we have to look for its causes, on the one hand, in the condition and supply of the blood, and on the other, in the formative capacity of the tissues themselves.—The Atrophy dependent upon an insufficient supply of nutritive materials may be either general or partial. General atrophy, or emaciation, is a necessary result of deficiency of food; but it may also proceed from an imperfect performance of the assimilating processes, whereby the nutritive materials do not receive their requisite elaboration, as in cases of disease of the mesenteric glands; or from an unusual energy of the metamorphic processes, whereby the azotized constituents of the food are decomposed into excrementitious products, without

undergoing assimilation at all, as seems to be the case in diabetes. Of the atrophy of a particular tissue, consequent upon the deficiency of its proper materials in the blood, we have an example in the reduction of the adipose tissue, when there is no surplus of fatty matter to serve for its nutrition, but, on the other hand, a withdrawal of the contents of the fat-cells into the circulating current, whilst the nutrition of the muscular and other azotized tissues may proceed with its usual vigour.—Instances of complete local atrophy, or gangrene, resulting from deficiency in the supply of blood to a part, are by no means unfrequent; but it is less common to meet with a prolonged diminution in the rate of nutrition from such a cause, since a partial obstruction to the circulation is usually removed after a short time by the enlargement of the collateral vessels. Yet there are peculiar circumstances under which this does not take place; thus Mr. Curling has shown that atrophy may occur in that portion of a fractured bone which is cut off from the direct supply of blood through the great nutrient artery; the circulation being restored by anastomosis to such an extent as to prevent the death of the bone, but not so completely as to support vigorous nutrition.*

332. The most frequent cause of Atrophy lies, however, in the deficiency of formative power in the tissues themselves, arising from the decline of that capacity which they inherit from the germ. This decline, as already shown, takes place in the body at large, as a part of the regular order of things, with the advance of years, and also normally occurs in particular organs at earlier periods of life; but it sometimes takes place prematurely, either in the body at large, or in particular organs, so that they undergo a wasting or degeneration without any ostensible cause. Thus it is not at all uncommon for Articular Cartilages to be almost entirely destroyed through defect of nutrition, without any pain or other symptoms to call attention to the change in progress;† and many similar cases might be cited. There is reason to believe that 'fatty degeneration,' the form under which degeneration most commonly presents itself, is in reality far more frequent than simple wasting; but it attracts less notice, because the bulk of the tissue is little or not at all diminished; and it is only when their function becomes impaired that attention is seriously drawn to the change. This form of Atrophy can seldom be attributed to antecedent diminution in functional activity; for it is most common in organs upon which there is the most constant demand for the energetic performance of their respective duties, as, for instance, in the heart, the kidneys, and the liver. But the formative activity of Muscles and Nerves is so closely dependent, as already several times pointed out, upon the active exercise of their functional powers, that atrophy is certain to supervene if this be interrupted; and this atrophy may or may not present itself under the form of fatty degeneration; a shrinkage of the parts, concurrently with the production of an increased amount of fat in them, being perhaps the mode in which it most frequently takes place. Atrophy of one part, moreover, may be dependent upon atrophy or imperfect functional activity of another, if the two be so related in their normal functions, that a decline of one involves a corresponding decline in the other. Thus, if a motor nerve be paralysed, the muscles which it habitually calls into action will be atrophied; and this will equally happen, whether the want of motive power depend upon a deficient production of it in the nervous centres, or upon an interruption to its conduction through the trunks. On the other hand, if the muscles of a part undergo degeneration from want of use (as in disease of the hip-joint), the

* "Medico-Chirurgical Transactions," vol. xx.

† See Redfern, "On Abnormal Nutrition in Articular Cartilages," p. 65.

nerves which supply them also suffer. The same is the case in regard to the nerves and organs of sense; for atrophy of the eye will occasion atrophy of the optic nerve, and destruction of the optic ganglia will induce atrophy of the eyes and optic nerves. Even the bones of a limb will suffer, in cases of atrophy of the muscles consequent upon disuse; for in an experiment made by Dr. J. Reid, to determine the effect of artificial exercise in maintaining the nutrition of muscles whose nerves had been divided, the bones of the quiescent limb only weighed 81 grains, whilst those of the exercised limb weighed 89 grains.*—It is an important fact, which was first pointed out by Sir J. Paget,† that when fatty degeneration is commencing in any tissue, which is characterized by the persistence of its nuclei, it is in the nuclei that the first alterations are seen; for they become pale and indistinct, and may even disappear altogether, almost before any other change is discernible in the contents of the cells or tubes to which they appertain; but in atrophy from mere decrease, this disappearance of the nuclei does not occur.

333. *Reparative Process.*—The nutritive operations take place with extraordinary energy and rapidity in the process of *Reparation;* by which losses of substance occasioned by injury or disease are made good. In its most perfect form, this process is exactly analogous to that of the *first development* of the corresponding parts; and its results are as complete in the one case as in the other. In fact, among the lowest tribes of Animals, we find these two conditions blended, as it were, together; for the process of reparation may be carried in them to such an extent, as to reproduce the whole organism from a very small portion of it. In the Hydra, or Fresh-water Polype, there would seem to be scarcely any limit to its power; for, even if the body of the animal be minced into small fragments, every one of these can produce a new and perfect being. In this manner, no less than forty have been artificially generated from a single individual.—In ascending the Animal scale, we find this reparative power less conspicuous, because limited in its exercise to particular tissues and to comparatively insignificant parts of the body;‡ and in Man, as in other warm-blooded Vertebrata, the regenerative power is for the most part restricted in its exercise, as Sir J. Paget has pointed out,§ to three classes of parts;—namely, (1.) "Those which are formed entirely by nutritive repetition, like the blood and epithelia (their germs being continually generated *de novo* in the ordinary condition of the body); (2.) Those which are of lowest organization, and (what seems of more importance) of lowest chemical character, as the connective tissues and the bones; (3.) Those which are inserted in other tissues, not as essential to their structure, but as accessories, as connecting or incorporating them with the other structures of vegetative or animal life, such as nerve-fibres or blood-vessels. With these exceptions, injuries or losses are capable of no more than repair in its limited sense—*i.e.*, in the place of what is lost, some lowly-organized tissue is formed, which fills up the breach, and suffices for the maintenance of a less perfect life."—Yet, even thus restricted, the operations of this power are frequently most remarkable; and are in no instance, perhaps, more strikingly displayed, than in the re-formation and re-modelling of an entire Bone, when the original one has been destroyed by disease. That this power is intimately related to that by which the organism is normally built up and maintained is evident, not merely from the peculiar mode in which it is exercised—its tendency being always to reproduce each part in the form and structure characteristic of it at the particular period of

* "Physiological, Anatomical, and Pathological Researches," p. 10.
† "Lectures on Surgical Pathology" vol. i. p. 106.
‡ See "Princ. of Comp. Phys.," chap. xi. sect. 3. § Op. cit., p. 164.

life, and not according to its embryonic type—but also from the fact that it is more effectual in the state of growth than in the adult condition, and that it can do far more in the embryonic state, when development as well as growth is taking place, than after the developmental process has ceased. In fact, as Sir J. Paget has remarked (loc. cit.), its amount at different periods of existence, as in different classes of animals, seems to bear an inverse ratio to the degree of development which has already taken place. Thus it is well known to every practitioner, how much more readily and perfectly the lesions resulting from accident or disease are repaired in childhood and youth, than they are after the attainment of the adult state. And there is evidence that during embryonic life, the regeneration of lost parts may take place in a degree to which we have scarcely any parallel after birth; for Professor Simpson* has brought together numerous cases in which, after "spontaneous amputation" of the limbs of a fœtus, occurring at an early period of gestation, there has obviously been an imperfect attempt at the re-formation of the amputated part from the stump; and it seems probable, from the history of normal development, that in the cases in which perfect hands and feet have been present without the corresponding limbs, these hands and feet have been secondary productions from the stumps of amputated limbs, since any original defect of development would have affected the hands and feet rather than the arms and legs. There are occasional examples, moreover, in which this regenerative power has been prolonged to an unusually late period; thus an instance is recorded, on authority that can scarcely be doubted, of the twice repeated reproduction of a supernumerary thumb, after it had been twice completely removed;† and the Author has been assured by a very intelligent surgeon, that he was cognizant of a case in which the whole of one ramus of the lower jaw having been lost by disease in a young girl, the jaw had been completely regenerated, and teeth were developed and occupied their normal situations in it.‡

334. The regeneration of epithelium when the injury has been so slight as only to effect its abrasion has chiefly been studied in the case of the corneal epithelium,§ and appears to be effected chiefly by the adjoining cells thrusting out processes towards the wound and gradually bridging it over and covering it; but some new cells may also arise from the multiplication and development of the nuclei in the subjacent tissue, and there give rise to the formation of islands (Küss). The importance of the artificial aid that may be given to the efforts of nature in this direction are sufficiently shown in the remarkable results obtained by Reverdin in his method of treating ulcers by the transplantation of skin.‖ The reparation of somewhat deeper wounds, in which there has been so great a loss of substance that neither immediate union nor adhesion by a thin layer of coagulable lymph can take place, is accomplished by the gradual development of new tissue from the 'nucleated blastema' with which

* These cases were brought by Professor Simpson before the Physiological Section of the British Association, at its Meeting in Edinburgh, Aug. 1850. The Author, having had the opportunity of examining two living examples, as well as Professor Simpson's preparations, is perfectly satisfied as to the fact.

† See Mr. White's Treatise on the "Regeneration of Animal and Vegetable Substances" (1785), p. 16. A case was under Dr. Carpenter's observation, where the reproduction of a supernumerary digit, after removal, occurred *once*, and a second operation was postponed till the child had ceased to grow.—Ed.

‡ For analogous cases, see Wagner "On Resections," Sydenham Society's transl., p. 137.

§ See Arnold, Virchow's "Archiv," Band xlvi. Heft 2; Hoffmann, idem, 1870, p. 373; Heiberg, Stricker's "Jahrbücher," 1871, p. 7, and Küss, "Cours de Physiologie," 1872.

‖ Reverdin, "Archives Gén. de Méd.," 1872, Mars, Juin. Duval, "Nouveau Dict. de Méd.," 1873, t. xvi. p. 715. Demarquay, "De la Régénération des Organes et des Tissues," 1874, p. 61.

the cavity is first filled. But this may take place in different modes, according to the degree in which it is disturbed by the Inflammatory process; and it should be the great object of the Surgeon to procure the most favourable method of its performance. It has been shown by Sir J. Paget* that the mode in which the process of filling up is accomplished differs essentially according as the wound is subcutaneous or is exposed to air. In the former case, the nucleated blastema is gradually developed into fibrous tissues without any loss, and usually with freedom from local inflammation (beyond what may have been requisite for the production of the plastic fluid), as well as from constitutional irritation. In the latter case, the nucleated blastema is developed into cells; and those on its exposed surface are unable, either from degeneration or from imperfect development, to pass on to any higher form of organization, but take on the characters of pus-cells, and are only fit to be cast off.† Hence there is a continual loss of plastic material, the amount of which in the case of an extensive suppurating sore, forms a most serious drain upon the system; whilst at the same time the local inflammation gives rise to more or less of constitutional disturbance, and the formation of new tissue is by no means so perfect as in the preceding case. In cold-blooded animals, however, the contact of air does not produce this disturbance; and we see wounds with extensive loss of substance gradually filled up in them by the development of new tissue, without any suppuration or other waste of material, very much as in the subcutaneous wounds of warm-blooded animals.

335. The most effectual means of promoting this kind of Reparative process, and of preventing the interference of Inflammation, vary according to the nature of the injury. The exclusion of air which almost invariably contains the germs of low organisms from the surface, and the regulation of the temperature, appear the two points of chief importance. The value of the former is well shown by the favourable results obtained by the plan suggested by Professor Lister,‡ of dressing wounds in an atmosphere saturated with carbolic acid spray and of the free application of carbolic acid to wounds, fistulous passages, &c., and by covering them with a paste formed of whiting, boiled linseed-oil, and carbolic acid.

CHAPTER XI.

OF SECRETION AND EXCRETION.

1. *Of Secretion in General.*

336. The literal meaning of the term Secretion is *separation;* and this is nearly its true acceptation in Physiology. But the ordinary processes of Nutrition involve a separation of certain of the components of the Blood, which are withdrawn from it by the appropriating power of the solid textures; and every such removal may be considered in the light of an act of *excretion*, so far

* Op. cit.

† The organizable material or lymph containing pus-corpuscles thus thrown out, constitutes a very favourable bed for the development and multiplication of the various spores which the researches of Tyndall ("Nature," vol. i. 1869–70, p. 339, and vol. iv. p. 124), as well as those of Dr. Cunningham and Lewis (Reports, Sanitary Board of Calcutta), have shown to be constantly floating in the air. At the temperature of the body, Bacteria, Vibriones, and other organic forms soon make their appearance in incalculable numbers, and accompany, if they do not produce, the putrefaction which takes place in the fluid. Burdon Sanderson, 'Lectures on Comparative Pathology,' "Brit. Med. Journal," 1877–78.

‡ "Lancet," 1867, pp. 326, 357, &c.

as the blood and the rest of the organism are concerned. Moreover, the separation of certain matters from the blood in a fluid state, either for the purpose of being cast forth from the body, or of being employed for some special purpose within it, which constitutes what is ordinarily known as Secretion, is effected by an instrumentality of the same nature with that whose operation constitutes an essential part of the nutritive process—namely, the production and subsequent agency of cells. Hence there is no other fundamental difference between the two processes, than such as arises out of the diverse *destinations* of the separated matters, and from the anatomical arrangements which respectively minister to these. For the products of the Secreting action are all poured forth, either upon the external surface of the body, or upon the lining of some of the cavities which communicate with it; and the cells by which they are separated from the blood usually stand in the relation of epithelium-cells to those prolongations of the skin or of mucous membranes, that form the follicles or extended tubuli of which the Glandular organs are for the most part composed. The act of Secretion appears to consist, in some cases, in the successive production and exuviation of the cells which minister to it, these cells giving up, by rupture or deliquescence, the substances which they have eliminated from the blood; such, for example, appears to be the mode of separation of the Sebaceous secretion of the skin, of the secretion of Milk, and perhaps also of the Biliary secretion. On the other hand, there can be little question that those more liquid secretions, in which there is either very little solid matter (as is the case with the Cutaneous transpiration and the Lachrymal fluid), or in which the solids, though in larger amount, are in a state of such perfect solution as to be capable of easy transudation (as is the case with the Urine), are not formed in this mode; since neither are exuviated cells normally found in the secreted fluids, nor do the epithelial cells lining the glandular tubes or follicles present indications of being in a state of continual change. The observations of Heidenhain and Langley are very instructive in this respect, for they show that in the case of the salivary glands, the cells lining the acini, when exhausted by secretion, are small, dark, and full of protoplasm, whilst after prolonged rest they are much larger and brighter, are no longer capable of being stained with carmine, and the protoplasm occupies a portion of the cell, where it appears in the form of the demilune of Giannuzzi. In this and similar cases, it seems fair to conclude that the *selective* powers of the cells are due to the protoplasm they contain; which during the period of rest is employed in elaborating from the surrounding blood or lymph the special secretion of the gland, and which under the influence of the nervous system swells up and causes the discharge of the contents of the cell, either by rupture, or, as seems more probable, by transudation.* However this may be,

* Giannuzzi, "Ber. d. Kön. Sächs. Gesell. d. Wiss. Sitz.," Nov. 27, 1865, suggested that in the case of the salivary secretion there is first an increased filtration of water from the blood into the lymph spaces, and secondly, a filtration of the water into the gland spaces. The former he thought was a mechanical result of the increase of the blood pressure in the capillaries when the chorda tympani was stimulated, whilst the latter was attributable to increased activity of the gland cells, consequent on stimulation of the true secretory nerves. But Heidenhain (Pflüger's "Archiv," Band xvii. 1878, p. 53) points out that stimulation of the chorda and of the nerve of Jacobson in atropinized rabbits, ought to cause œdema of the salivary glands, since this drug arrests secretion, whilst it does not interfere with the increased activity of the circulation, nor lead to any remarkable augmentation in the discharge of lymph through which channel any surplus fluid transuded through the walls of the distended vessels might be expected to escape. Hering ("Sitz. d. Wiener Akad.," Band lxvi.; Abt, vol. iii. 1872, p. 83) believed that in the case of the salivary glands, a colloidal substance like mucin, with high powers of imbibition, was produced in the gland

each group of cells is adapted to separate a product of some particular kind, which constitutes its special *pabulum;* and the rate of its production seems to depend, *cæteris paribus*, upon the amount of that pabulum supplied by the circulating fluid. The substances at the expense of which the secreting cells grow, however, may not be precisely those which are subsequently cast forth; for it is very probable that some of them at least undergo a certain degree of chemical transformation by the agency of these cells; the characteristic materials of the several secretions not being always found to pre-exist *as such* in the blood.

337. A distinction may be drawn as regards this point, between those *Excretions*, the retention of whose materials in the Blood would be positively injurious, and those *Secretions*, which are destined for particular purposes within the system, and the suspension of which has no immediate influence on any other functions than those for which they are respectively destined. The solid matter dissolved in the fluids of the latter class is little else than a portion of the *nutritive* constituents of the Blood; either so little altered as still to retain its nutritive character, as is the case with the casein of Milk, and with the albuminous constituent of the serous fluid of areolar tissue and of serous and synovial membranes; or in a state of incipient retrograde metamorphosis, as seems to be the case with the peculiar "ferments" of the salivary, gastric, pancreatic, and intestinal secretions. On the other hand, the characteristic ingredients of the Excretions are very different in character from the normal elements of the blood. They are all of them completely unorganizable; and they possess, for the most part, a simple atomic constitution. Some of them also have a tendency to assume a crystalline form; which, as Dr. Prout justly remarked, indicates their unfitness to enter into the composition of organized tissues. With regard to some of the chief of these, there is sufficient evidence of their existence, in small quantity, in the circulating Blood; but it is also clear that they exist there as products of decomposition, and that they are destined to be separated from it as speedily as possible. If their separation be prevented, they accumulate and communicate to the circulating fluid a positively deleterious character. Of this, we have already seen a striking example in the case of Asphyxia; and the history of the other two principal Excretions, the Bile and Urine, will furnish evidence to the same effect.—As a general fact, then, it may be affirmed, that the materials of the proper Excretions pre-exist in the Blood, in a state nearly resembling that in which they are thrown off by the secreting organs; and that, as their presence there is the result of the destructive changes that have taken place in the system, they cannot be retained in it without injury; but that the materials of those Secretions which are destined to perform some particular function within the economy, are derived from the nutritive substances which are appropriated to its general purposes.

338. Notwithstanding that, under ordinary circumstances, the several parts of the Excretory apparatus are limited, each to its own special function, we find that there are certain *complementary* relations between them, which makes the action of one vicarious to a certain extent with that of another. Such a relation seems to exist, for instance, between the Lungs on one side, and the Liver and Intestinal glands on the other: for, the more active the respiration, the less bile is secreted; whilst, if the respiration be lowered in amount

cells, and that this seized the water, and, dissolving in it, formed the secretion, which was discharged under comparatively high pressure; but Heidenhain again objects, that the pressure under which the saliva is secreted by the different glands bears no relation to the amount of mucin the cells contain. See Langley, "Journal of Physiology," vol. ii. 1879, p. 261; and Langley and Sewall, ibid. p. 281.

by inactivity of body and a high external temperature, a larger proportion of unoxidised or imperfectly oxidized excrementitious matters accumulates in the blood, giving rise to that augmented production both of the biliary and of the fæcal excretions, which constitutes diarrhœa.* And thus, on the other hand, when the liver is not adequately effecting the depuration of the blood from the constituents of bile, an augmentation of the respiration by active exercise in a low temperature gives most effectual relief.—Still more obviously vicarious, however, are the Kidneys and the Skin; for here we find that not only do the kidneys allow the transudation of whatever superfluous water may remain in the circulating current, after a sufficient amount has been exhaled from the skin to keep down the temperature of the body to its normal standard, but the skin actually assists in the elimination of one of those products of the metamorphosis of the azotised tissues, the removal of which has been until recently considered as the special function of the kidney. Consequently, whenever the due action of the skin as an excreting organ is interfered with, it is the kidney especially that will be called on to take its place; whilst, on the other hand, if it be thought desirable to relieve the kidney, this may be most effectually done by stimulating the skin to increased excretory activity. This vicariousness of function among the Excretory organs presents itself far more remarkably, however, in certain states of disease; in which a complete "metastasis of secretion" may exhibit itself. The capability of one organ thus to take upon itself the special action of another appears to be related to the "community of function" existing in the secretory surface among those lower animals which manifest none of the "specialization," or setting apart for particular offices, that we see in the higher; for it seems to be a general law in Physiology, that, even where the different functions are most highly specialized, the general structure retains, more or less, that primitive community of action which characterized it in the lowest grade of development.†

339. It is in regard to the *Urinary* excretion that the evidence on this point is most complete; for it seems to be established by a great mass of observations, that urine, or a fluid presenting its essential characters, may pass off by the mucous membrane of the intestinal canal, by the salivary, lachrymal, and mammary glands, by the testes, by the ears, nose and navel, by parts of the ordinary cutaneous surface, and even by serous membranes, such as the arachnoid tunic lining the ventricles of the brain, the pleura, and the peritoneum. A considerable number of such cases was collected by Haller;‡ many more were brought together by Nysten;§ and more recently Burdach‖ has furnished a full summary of the most important phenomena of the kind; and Dr. Laycock¶ has compiled a valuable collection of cases of urinary metastasis occurring as complications of hysteria. The following table of cases, referred to by the last of these authors, will give some idea of the relative frequency of the different forms of this curious affection:—

Vomit.	Stool.	Ears.	Eyes.	Saliva.	Nose.	Mammæ.	Navel.	Skin.	Total.
34	20	4	4	5	3	4	34	17	125

* Such is probably the occasion of the 'bilious attacks' and 'autumnal cholera' so prevalent at the close of the summer; the subjects of these being most commonly persons who have not reduced their consumption of food during the warm season, in accordance with the diminished demand for the production of heat within the body.

† See "Princ. of Comp. Phys.," §§ 110, 428. ‡ "Elementa Physiologiæ," tom. ii. p. 370.

§ "Recherches de la Physiologie et de Chimie pathologiques," p. 265.

‖ "Traité de Physiologie" (Jourdan's translation), vol. viii. p. 248, *et seq.*

¶ "Edinb. Med. and Surg. Journ.," 1838; and "Nervous Diseases of Women," p. 233.

It is to be borne in mind, however, that cases of hysterical ischuria are frequently complicated with that strange moral perversion which leads to the most persevering and ingenious attempts at deceit; and there can be little doubt that a good many of the instances on record, especially of urinous vomiting, are by no means veritable examples of metastasis.—The proofs of the fact we are seeking to establish are, therefore, much more satisfactory when drawn from experiments upon animals, or from pathological observations, about which, from their very nature, there can be no mistake. Thus Mayer* found that when the two kidneys were extirpated in the guinea-pig, the cavities of the peritoneum and the pleura, the ventricles of the brain, the stomach, and the intestinal canal, contained a brownish liquid having the odour of urine; that the tears exhaled the same odour; that the gall-bladder contained a brownish liquid not resembling bile; and that the testes, the epididymis, the vasa deferentia, and the vesiculæ seminales, were gorged with a liquid perfectly similar to urine. Chirac and Helvetius are quoted by Haller as having tied the renal arteries in dogs, and having then remarked that a urinous fluid was passed off from the stomach by vomiting. A considerable number of cases of the discharge of urine by exceptional means have been collected by Burdach.† In all the older statements of this kind, there is a deficiency of evidence that the fluids were really urinous, urea not having been obtained from them by chemical analysis, and the smell having been chiefly relied on. The urinous odour, however, when distinct, is probably nearly as good an indication of the presence of the most characteristic constituent of human urine, as is the appearance of the urea in its separated form. The passage of a urinous fluid from the skin has been frequently observed in cases in which the renal secretion was scanty; and the critical sweats by which attacks of gout sometimes terminate, contain urates and phosphates in such abundance as to form a powdery deposit on the surface.

340. The metastasis of the *Biliary* secretion is familiar to every practitioner, as being the change on which *jaundice* is dependent. It is not, however, in every case of yellowish-brown discoloration of the tissues, that we are to impute such discoloration to the presence of biliary matter; and we can only safely do so when we have at the same time evidence of concurrent obstruction of the biliary apparatus. The urinary apparatus then affords the principal channel through which the biliary matter is eliminated;‡ the urine becomes tinged with the colouring principle of bile, being sometimes of a yellowish or orange hue, and sometimes of a brown colour with a considerable sediment; and the presence of the most characteristic constituents of the bile has been determined in the urine. The same result presents itself when the biliary duct has been artificially obstructed by ligature. Other secretions have been found tinged with the colouring matter of bile; thus the pancreatic fluid has been seen of a yellow colour in jaundice; and the milk has presented not merely the hue, but the characteristic bitterness, of the biliary secretion. The cutaneous transpiration is not unfrequently so much impregnated with biliary matter, as to communicate its tinge to the linen covering the skin; and even the sputa of patients affected with bilious fevers have been observed to be similarly coloured, and have been found to contain biliary matter. The secretions of serous membranes, also, have been frequently seen to present the characteristic hue of bile; and biliary matter has been detected, by analysis, in the fluid of the pleural and peritoneal cavities. Biliary matter, however,

* "Zeitschrift für Physiologie," Band ii. p. 270. † Ibid. Band ii. pp. 253, 254.
‡ See J. W. Legg in "St. Barthol. Hospital Reports," vol. ix. p. 161.

when unduly present in the circulating current, is not removed from it by the secreting organs alone; for it seems to be withdrawn also in the ordinary operations of nutrition, entering into combination with the solid tissues. Thus, in persons affected with jaundice, we find the skin, the mucous and serous membranes, the lymphatic glands, the brain, the fibrous tissues, the cartilages, the bones and teeth, and even the hair, penetrated with the colouring matter of the bile, which they must have withdrawn from the blood, and which seems to have a particular affinity for the gelatinous tissues. It is impossible at present to say, however, to what extent the more characteristic ingredients of the bile are thus withdrawn from the blood; for the presence of its *colouring matter* cannot by any means be taken as an indication that its peculiar *resinoid acids* are also incorporated with the normal components of the tissues.

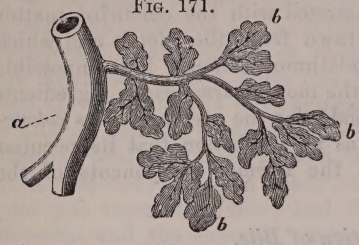
2. *The Liver.—Secretion of Bile.*

341. The Liver is only certainly known to be present in Vertebrate animals, for though in many Invertebrata large glands exist which pour the products of their secretion into the intestines, and may probably, especially when of a yellow colour, resemble bile in their action on the food, they have not as yet been shown to present the characteristic structure of the liver, nor to contain either true biliary colouring matter, nor, which is of much greater importance, the biliary acids; whilst other glands discharge their contents into the intestines, to which the function of secreting a biliary fluid might with equal reason be assigned. Even in the Amphioxus, the lowest of the Vertebrate series, no liver is present. In all other Vertebrated animals the Liver seems to be constructed on one and the same plan. Its component cells, which have not been proved to possess a definite cell-wall, are contained in distinct cæcal follicles, or elongated tubuli, branching off from the excretory ducts; but in ascending through the Vertebrated series, it presents a more and more solid parenchymatous texture. This character is very obvious in the liver of Man, which is peculiarly firm and compact, and has less of connective tissue between its different parts than is found in that of many other Mammalia.—It is observable, moreover, in the Human liver, that certain portions are rudimentary, which are elsewhere fully developed. The liver in Mammalia, as in the lower vertebrates, is essentially a bilobed organ, but this character is usually more or less concealed by the various accessory fissures by which it is divided into many lobes; always, however, on the same general plan. The fissure in which the umbilical vein runs constitutes the primary division into right and left segments. In the most complex forms usually met with in the Quadrumana, Carnivora, Insectivora, Rodentia, Edentata, Marsupialia, &c., the left segment is further divided by the *left-lateral fissure* into a *left-lateral* and a *left-central lobe*. The right segment is similarly divided into a *right-central* and *right-lateral lobe*; and it has, moreover, two accessory lobes on its under surface, the Spigelian and the caudate. When the gall-bladder is present it is attached to the under surface of the right-central lobe. In most Ungulates, in Cetacea, in the highest Apes, and in Man, the lateral fissures are not present, and the liver appears of simpler form. In Man the simplicity is further increased by the caudate being hardly distinguishable from the right-lateral lobe and the Spigelian lobe being but little developed.*

* See W. H. Flower 'On the Organs of Digestion of Mammalia,' "Med. Times and Gazette," March 9th, 1872, *et seq.* The weight of the Liver is from 48–58 ozs. in the male, and from 40–50 ozs. in the female. Its sp. gr. is about 1·05. From the examination of a large number of bodies, Steffan ("Jahrbuch f. Kinderheilk.," N. F. Band v. p. 47) found

342. When the liver is closely examined with the naked eye, it is seen to be made-up of a great number of small granular bodies, about the size of millet-seeds, of an irregular form, and presenting a number of rounded projecting processes upon their surfaces. These are commonly termed *lobules*, although by some Anatomists they are spoken of as *acini*.* When divided longitudinally, they have a somewhat foliated appearance (Fig. 171), arising from the distribution of the Hepatic Vein, which spreads from the centre of each division. When transversely divided, the lobules are usually found to present somewhat of a pentagonal or hexagonal shape, the angles being slightly rounded, so as to form a series of passages or interlobular spaces: in these lie the branches of the Vena Portæ (as well as of the Hepatic Artery and Duct), from which are derived the plexuses that are contained within the lobules. The exterior of each lobule is covered by a process of the 'capsule of Glisson,' which is very dense in the Pig and other animals but is so thin as to be almost indistinguishable in the Human Liver; the interspaces between the vessels are filled by the ultimate terminations of the Hepatic biliary ducts, which contain large secreting cells.† The structure of each lobule, then, gives us the essential characters of the whole gland.

Fig. 171.



Connection of the *Lobules of the Liver* with the Hepatic Vein:—*a*, trunk of the Vein; *b*, *b*, lobules depending from its branches, like leaves on a tree; the centre of each being occupied by a venous twig, the Intralobular Vein.

343. The supply of arterial blood, and therefore of loosely-combined oxygen to the liver, is remarkably small as compared with other organs. The diameter of the Hepatic Artery in man is only 5·6 millimetres (1-5th of an inch), whilst that of the Splenic Artery is from 6·2–6·8 mm., and that of the Renal Artery from 5·6 to 6·8 mm. Yet the relative weights of these three organs are—liver 1400–1900 grammes, spleen 120–250 grammes, and kidney 116–174 grammes. The *Hepatic Artery* sends branches to every part of the Liver, supplying the walls of the portal and hepatic veins, and of the hepatic ducts, as well as Glisson's capsule. The principal distribution of its branches, however, is to the lobules, which they reach, in the same manner as the portal vessels and biliary ducts, by spreading themselves through the interlobular spaces. There they ramify upon the interlobular ducts, and upon the capsular surface of the lobules, which they then penetrate; terminating for the most part in the portal venous plexus, though a very few small branches may be traced into the Hepatic plexus of capillaries. The whole of the blood, therefore, of the Hepatic Artery passes through the lobuli, and is subservient to the secretion of Bile. But if the liver be sparingly supplied with arterial, it receives a large amount of venous blood. The *Vena Portæ*, which is formed by the convergence of the veins that return the blood from the chylopoietic viscera, probably also receives the blood which is conveyed to the liver for the

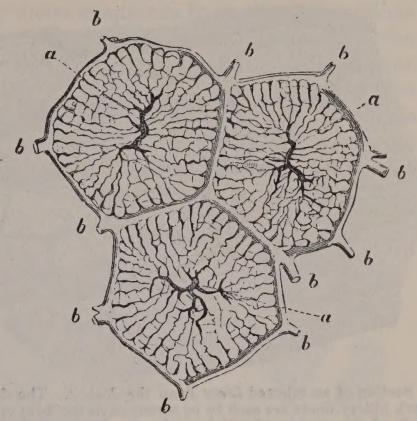
that the ratio of the weight of the Liver to the body weight is greatest after birth, and that it diminishes during the first year, especially in boys. In childhood the body weight and the liver weight increase, but not in equal proportion, the former augmenting most rapidly.

* The *acini* of Malpighi are the minute bodies of various forms and yellowish colour, which are seen when any individual lobule is examined with the microscope; these are nothing else, however, than the irregular islets of parenchyma, left between the meshes of the plexus formed by the ultimate ramifications of the portal vein.

† See Prof. Beale's paper 'On the Ultimate Arrangement of the Biliary Ducts,' in "Phil. Trans.," 1856, and Todd and Bowman's "Physiolog. Anat.," p. 459, vol. ii., 1859.

purposes of nutrition by the Hepatic Artery. Its diameter is 15·79 mm. Like an artery, it gradually subdivides into smaller and yet smaller branches; and at last it forms a plexus of vessels, which lie in the inter-lobular spaces, and spread with the freest inosculation throughout the entire Liver. To these vessels, the name of *inter*-lobular Veins was given by Mr. Kiernan.* They ramify in the capsules of the lobules, covering with their ramifications the whole external surface of these; and then enter their substance. When they enter the lobules, they are termed *lobular* veins; and the plexus formed by their convergence from the circumference of each lobule towards its centre is designated as the *lobular venous plexus*. The ultimate ramifications terminate in those of the intra-lobular, which discharge themselves into the sub-lobular veins, and through them into the hepatic vein. It now only remains to describe the *Hepatic Veins*, the branches of which occupy the interior of the lobules, and are termed *intra*-lobular veins (Fig. 172, *a*, *a*, Fig. 173). On making a transverse section of a lobule, it is seen that the central vessel is formed by the convergence of numerous minute venules, which arise from the plexus upon the surface of the lobule. The intra-lobular veins terminate in the larger trunks, which pass along the bases of the lobules, discharging into them their venous blood; these are called by Mr. Kiernan *sub-lobular* veins. The main trunk of the Hepatic Vein terminates in the ascending Vena Cava. The pressure of the blood in the Hepatic Veins varies from + 3 or 4 mm. to − 7 mm. of Mercury, whilst it amounts to between + 7 and + 16 mm. in the Vena Portæ,† and the time occupied by the circulation of a given quantity of blood through it is probably not far short of that taken up by the major circulation, *i.e.*, from the crural vein to the crural artery.‡

Fig. 172.



Horizontal section of three superficial Lobules, showing the two principal systems of *Blood-vessels*:—*a*, *a*, *intra*-lobular veins, terminating in the Hepatic veins; *b*, *b*, *inter*-lobular plexus, formed by branches of the Portal vein.

Fig. 173.

Section of a small portion of the *Liver* of a *Rabbit*, with the Hepatic or intra-lobular veins injected.

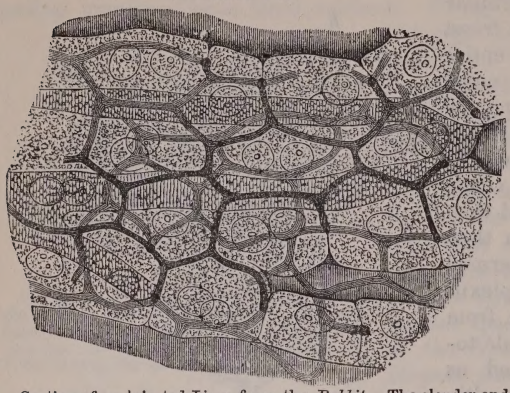
* See his admirable Memoir 'On the Anatomy and Physiology of the Liver,' in the "Philosophical Transactions," 1833.

† Rosapelli, "Récherches sur la Circulation du Foie," Paris, 1873.

‡ Flügge, "Zeitschrift f. Biologie," Band xiii. p. 133, 1877. It may be here mentioned that in this paper, which was overlooked by the Editor when page 263 was in the press, Flügge

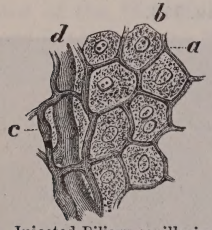
344. The *Hepatic Duct* forms, by its subdivision and ramification, an inter-lobular plexus very like that of the portal vein; the branches ramifying upon the capsular surface of the lobules, and ultimately penetrating into the interior (Fig. 174). The trunk and larger branches of the biliary duct consist of an internal mucous membrane and an external fibrous sheath. The former is very vascular and is lined by tall columnar cells; the latter is believed by Hering to contain smooth muscular fibres, arranged longitudinally, and a few blood-vessels; Asp, however, believes the spindle-cells and striated appearance relied upon by Hering, Heidenhain, and others, as evidence of muscular fibres to be due to elongated nuclei and connective tissue fibres, as they swell up and disappear in weak solution of hydrochloric acid and alcohol. At the point where the inter-lobular ducts become continuous with the network within the lobules, their diameter is very small, not exceeding 1–4000th to 1–5000th of an inch; and here the

Fig. 174.



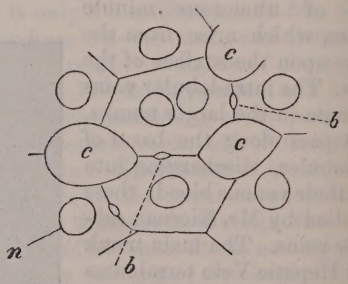
Section of an injected *Liver* from the *Rabbit*. The slender and dark biliary ducts are seen to be arranged in the form of a plexus, each of the meshes of which encloses a hepatic cell with one or two nuclei. The much wider capillaries are also shown.

Fig. 175.



Injected Biliary capillaries of the *Liver* of the *Rabbit*. Part of a Lobule, showing the arrangement of the biliary ducts in relation to the hepatic cells:—*a*, terminal plexus of biliary ducts; *b*, hepatic cells; *c*, biliary ducts; *d*, capillary blood-vessels.

Fig. 176.



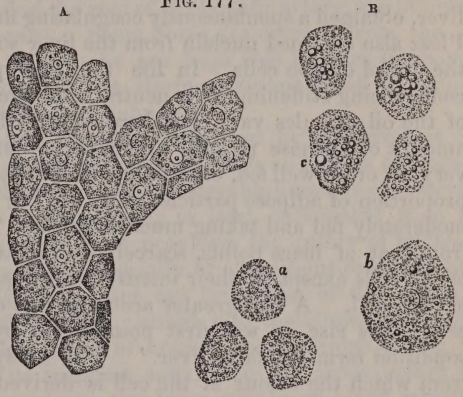
Section of *Rabbit's Liver* injected:—*c*, blood capillaries; *b*, bile passages; *n*, nucleus of hepatic cell.

epithelium, which in the medium-sized ducts remains columnar, passing in the smaller ducts into the tessellated variety, suddenly becomes spheroidal, or assumes the form of the true secreting cell. The tubes, of the diameter of 1–80th of an inch and larger, present many little saccular dilatations of the coats, the openings of which, according to Dr. Beale, are regularly arranged in two rows or lines on opposite sides of the ducts; and besides these are numerous small, irregular, and anastomosing canals, which run obliquely in the coats of the ducts, and ultimately open into their cavities.

states he has repeated Lehmann's experiments, and is unable to confirm them. He thinks that there is no perceptible difference between Portal venous and Hepatic venous blood.

These tubes and cæca may be regarded as accessory gall-bladders, in which the bile, secreted and stored up, comes into intimate relation with a fine plexus of capillaries, and may perhaps undergo further elaboration. In regard to the mode of termination of the finest biliary ducts it appears from the observations of Hering and others,* that, when injected, the canals existing between the large secreting cells form a close plexus (Fig. 175,*a*), the meshes of which appear to enclose the hepatic cells, though in reality the lines of injection follow the spaces between the large secreting cells (Beale). In the Rabbit these canals run exclusively, and in Man and the Dog in by far the greatest number, not along the angles, but between the opposite surfaces (Fig. 176) of two adjacent cells, dividing their surfaces sometimes into two equal halves and at others unequally. The blood capillaries (Fig. 176, *c*), on the other hand, chiefly run in the angles formed by the junction of three or more cells. According to Hering, the biliary canals and passages do not possess any membrana propria, their walls being formed by the hepatic cells themselves, which succeed suddenly to the flattened polyhedric cells of the smaller biliary ducts, but MacGillavry and Chrzonsczsczewsky maintain that they have proper walls, the bile secreting cells lying (Fig. 175) to their outside, though this is perhaps illusory, the supposed vascular wall being only a thickening of the cell-wall. Both Weber and Asp, from injections with gamboge dissolved in spirit (Weber), and alkanet in turpentine (Asp), have observed that under moderate pressure the fluid injected will often penetrate directly from the smaller biliary ducts into the biliary cells, the so-called biliary capillaries then entirely disappearing, and the peripheric part of the lobules becoming deeply stained; on subsequently injecting Prussian blue, Asp found that it was retained in the passages it would under ordinary circumstances have run in, and did not enter the cells, precluding, in his opinion, the idea that there are any coarse openings between the biliary ducts and liver cells. The demonstration of the ultimate biliary canals by the injection of coloured fluids is extremely difficult in Man, on account of the coagulation of their contents soon after death. They have, however, been very distinctly seen as the result of disease in animals,† and may perhaps hereafter be in this way made apparent in the human subject.

FIG. 177.



A, portion of a *Hepatic Column*, from Human Liver, showing its component secreting cells; B, secreting cells detached, *a*, in their normal state, *b*, a cell, more highly magnified, showing the nucleus and distinct oil-particles, *c*, in various stages of fatty degeneration.

345. The *biliary cells* of the Human liver (Fig. 177, *b*) are usually of a

* Stricker's "Manual of Histology," vol. ii. 1872, Syd. Soc. Translation. See also MacGillavry; "Sitz.-ber. d. k. Akad. zu Wien.," Band l. 1864. Reichert, in Reichert's "Archiv," 1866, p. 734. Irminger and Frey, in Kölliker's "Zeitschrift," 1866, p. 208. Oscar Wyss, in Virchow's "Archiv," 1866, April, and Chrzonsczsczewsky's paper abstracted in Humphry and Turner's "Journal," vol. i. 1867, p. 146. Kölliker, "Handbuch der Gewebelehre," 1867. Eberth, "Centralblatt," 1866, No. 57, and "Sitz.-ber. d. Wien. Akad.," Dec. 1866. A. Mayer, Stricker's "Med. Jahrbücher," 1872, p. 133, and Asp, l. c.

† "Texas Cattle Disease." Austin Flint, "Physiology of Man," vol. iii. p. 245.

polyhedric spheroidal form, channelled at their angles by the capillaries, and on their surfaces by the biliary canals, and are from 1–500th to 1–2000th of an inch in diameter. Each of them, generally, but not always (Asp), presents one or two distinct nuclei containing numerous granules; and the cavity of the cell is occupied by yellow amorphous biliary matter, usually having one or two large adipose globules, or five or six small ones, intermingled with it (Fig. 177, *a*, *b*). The biliary cells contain albuminous substances, which, after death, yield a globulin, an albumin coagulating in a weak neutral saline solution, at a temperature of 45° C. (113° F.), and another albuminous substance which dissolves very slowly in dilute solution of soda, and hence cannot be identical with alkali albuminate. Plosz, by freezing, mincing and pressing the liver, obtained a spontaneously coagulating fluid, as Kühne did from the muscles. Plosz also obtained nuclein from the liver substance, which was derived from the nuclei of the cells. In life the liver parenchyma is alkaline, but after commencing stiffening, it is neutral, and finally acid. The size and number of the oil globules vary considerably, according to the nature of the food, the amount of exercise recently taken, and other circumstances. If an animal be very fat or be well fed, especially with farinaceous or oleaginous substances, the proportion of adipose particles (Fig. 177, *c*) is much greater than in an animal moderately fed and taking much exercise. The size of the oil-globules varies from that of mere points, scarcely distinguishable from the granular contents of the cells except by their intense blackness, up to one-fourth of the diameter of the cell. A still greater accumulation of adipose particles in the biliary cells gives rise, as was first pointed out by Mr. Bowman,* to the peculiar condition termed "fatty liver." The finely granular matter is the portion from which the colour of the cell is derived; it seems to fill the space not occupied by the oil-globules; and it often obscures the nucleus, so that the latter cannot be distinguished until acetic acid is added, which makes the granular matter more transparent without affecting the nucleus.†—The Liver, therefore, belongs to the class of ramified tubular glands; and the materials of the biliary secretion formed from the blood by the cells lining the intralobular extremities of the ducts are discharged into the interior of these canals, either by exudation or by the deliquescence of the cells themselves. Teichmann‡ describes the lymphatics as running with the portal venous branches, and the biliary ducts as forming a plexus with large, irregular meshes on the outside of the lobuli, and he believes he has even injected minute branches passing up their centre with the Vena intralobularis of the Hepatic Veins.

* "Medical Gazette," Jan. 1842.

† Schiff ("Archiv f. Phys. Heilk.," 1857, p. 263, and "Untersuch. üb. die Zuckerbildung in der Leber," &c., Wurz. 1859) described two kinds of granules in the Liver cells besides the nucleus; one of these was dark-bordered and highly refractile, the other much smaller and pale. These last he thought were particles of Glycogen. Bock and Hoffman (Virchow's "Archiv," 1872, Band lvi. p. 202) deny this on the grounds of their chemical reaction and the want of relation between their numbers and the amount of Glycogen in the Liver, and believe that it exists in the form of a homogeneous mass. For an account of the albuminous compounds of the Liver, see Plosz, Pflüger's "Archiv," 1873, Band vii. p. 371. Schenk ("Centralblatt," 1869, p. 865) has described peculiar protoplasmic masses resembling amœbæ in possessing spontaneous movement, as being present in the embryonal Liver of mammals, and Pflüger ("Archiv f. ges. Physiol.," Band ii. p. 459) states that the liver cells possess processes like those of the salivary cells, and appears to think there is some communication between the biliary canaliculi and the interior of the cells; since, if the capillary ducts of the biliary canals are injected with cold Prussian blue injection, fine ducts may be seen to penetrate the protoplasm of the cells, which divide and surround the uncoloured nucleus. MacGillavry had previously noticed that on injection of the lymphatics with cold Prussian blue the *nuclei* of the colourless hepatic cells became deeply stained.

‡ "Saugader System," p. 94, Leipzig, 1861.

MacGillavry* describes the lymphatics of the liver of the rabbit as forming loose sheaths to the vessels, and his statements have been confirmed by Asp. Similar sheaths have been observed by Irminger and Frey around the blood-vessels of the liver of the dog. Wendt is of opinion, from physiological injections of Prussian blue, that is, the injection of colouring matter into the Veins of the living animal, the Venæ Portæ being tied, that in the guinea pig the finest roots of the lymphatic system are continuous with the commencement of the biliary ducts. A single layer of lymphatics exists on the peritoneal surface of the liver, lying in the subserous areolar tissue. The nerves of the Liver have been carefully examined by Dr. Robert Lee,† Hering,‡ and Pflüger.§ Dr. Lee has shown them to arise chiefly from the semilunar ganglion and sympathetic plexus surrounding the root of the hepatic artery, the minutest branches of which they accompany. Some fibres are derived from the left pneumogastric nerve. Pflüger believes he has been able to trace the nerves into connection with the hepatic cells, but Hering maintains that all demonstrable nerves lie on the outer side of the lobules.

346. The first and most obvious function performed by the Liver is the secretion of Bile. For this the arrangement of the cells and ducts appears to be primarily designed; and by their means a considerable quantity of material, rich in carbon and hydrogen, is, temporarily at least, eliminated from the blood, whilst at the same time a liquid is provided, the utility of which in promoting the absorption of food, and especially of oleaginous food, has been already sufficiently considered (§ 128). But the large size of this organ in comparison with the amount of secretion poured into the alimentary canal; its constant presence in almost all classes of animals, how various soever the nature of their food may be; its manifest activity in the fœtus before the ingestion of any food has taken place; the large supply of blood which it receives from different sources, as well as the peculiar relations which it holds to the blood returning from the placenta in the fœtus, and from the abdominal viscera in the adult—are all circumstances suggesting that other functions than the secretion of the Bile are here performed; and from the results of comparatively recent research it may now be considered as fairly established, that it exerts an assimilative or elaborating action on the freshly-absorbed materials of our food, and especially upon the albuminous and saccharine constituents, whereby they become more fitted for the nutrition of the body; and that in the course of these assimilative changes, the activity of which is indicated by the high temperature of the organ, and is perhaps a consequence of them, a material analogous to starch—glycogen—is formed, whose ultimate destination is still undetermined, but which there is some reason for believing in part, either directly or indirectly, combines with oxygen, and thus becomes subservient to the maintenance of animal heat, and in part is on the way to histological formation. The production of this substance is termed Glycogeny, and will be considered after the characters and mode of formation of the Bile

* MacGillavry, "Zur Anat. der Leber," Pamphlet, 1864. His statements are corroborated by Frey, "Handb. der Histol. und Histochem.," 4 Auf. p. 524, and Biesiadecki, "Wien. Sitzungsber.," Band lv. H. D. Schmidt in "Month. Micros. Journ.," 1870, Asp, Ludwig's "Arbeiten," 1873, Band vii. p. 134. See also for Lymphatics of Capsule of Liver, Wedl, idem. Band lxiv. Abth. 1. Fleischl, "Ber die k. sächs Gesell. der Wiss.," May 7, 1874. Budge, "Über die Lymphgefässe der Leber," idem. 21 July, 1875, and Wendt, "Centralblatt f. d. Med. Wiss.," 1878, p. 260.

† Lee, "Proceedings of Royal Society," vol. xii. p. 246.

‡ Hering, Stricker's "Human and Comparative Histology," Syd. Soc. Trans., vol. ii. p. 33.

§ Pflüger, "Archiv f. Physiologie," Band iv. p. 53. For the lymphatics of the Gall-bladder, see M. Deutsch, "Centralblatt f. d. Med. Wiss.," 1876, p. 41.

have been discussed. The following are analyses of the Bile contained in the human Gall-bladder, by Frerichs and v. Gorup-Besanez:*—

In 1000 parts.	FRERICHS.		V. GORUP-BESANEZ.			
	I. Man æt. 18, killed by a fall.	II. Man æt. 22, killed by injury.	I. Man æt. 49, criminal, beheaded.	II. Woman æt. 29, criminal, beheaded.	III. Man æt. 68, killed by a fall.	IV. Boy æt. 12, killed by an injury.
Water	860·0	859·2	822·7	898·1	908·7	828·1
Solid residue	140·0	140·8	177·3	101·9	91·3	171·9
Biliary acids in combination with alkalies . .	72·2	91·4	107·9	56·5	73·7	148·0
Fat	3·2	9·2	47·3	30·9		
Cholesterin	1·6	2·6				
Mucus and colouring matter.	26·6	29·8	22·1	14·5	17·6	23·9
Salts	6·5	7·7	10·8	6·3	—	—

Bile is a viscid, neutral or feebly-alkaline, somewhat oily-looking liquid, of a greenish-yellow colour, and very bitter taste, followed by a sweetish after-taste. It is readily miscible with water, and in solution froths like one of soap. Its specific gravity in the human subject is about 1·018, the extremes being 1·0105 and 1·032. According to Kowalewsky† the pressure of the Bile in the ductus communis choledochus under ordinary circumstances in curarized cats, varies from 3·5 to 7·5 mm. of mercury (2–4 in. of water), rising if the duct be ligatured to from 12 to 20 mm. of mercury (6–11 in. of water). Heidenhain states that it is secreted under a pressure of a column of water, eight inches in height. The proportion of solid matter which it contains is usually from 9 to 17 per. cent., and nearly the whole of this consists of substances peculiar to Bile. 100 parts of human Bile purified and dried at 230° F. contain about 1·5 parts of sulphur. The gases of the Bile‡ are oxygen, carbonic acid, and nitrogen, but their proportion seems to vary within rather wide limits, being greatest if collected immediately after death. Thus the oxygen in the bile of the dog varies from 0 to 1·22 vol. per cent., carbonic acid capable of being removed by the air-pump from 0 to 19·5 vol., carbonic acid capable of being expelled by Phosphoric acid 0·6 to 62·5 vol., and Nitrogen from 0·4 to 9·13 vol. per cent. The constituents of the Bile are mucin, diastatic ferment, salts of biliary acids; the colouring matters, bilirubin and biliverdin, lecithin, cholesterin, urea, oleates, stearates and palmitates of the alkalies, as well as salts of certain volatile fatty acids; olein, palmitin, stearin, and various salts, as sodium chloride, and iron, magnesium and calcium phosphate. The biliary salts in man constitute about 6·5 per cent. of the bile, of which taurocholate of soda forms 1·5 parts, and glycocholate of soda 5 parts. Besides these salts substances insoluble in alcohol (chiefly mucin) constitute 3·5 parts, and soaps 1·5 per cent. The quantity of sulphur is about one-tenth per cent.,§ which is chiefly contained in the taurocholic acid, no less than 25 per cent. of that element existing in Taurin, so that the proportion

* "Phys. Chem.," 1875, p. 529. † Pflüger's "Archiv," Band viii. Heft xii.

‡ These have been examined by Pflüger, "Pflüger's Archiv," Band ii. 1869, p. 173; Bogoljubow, "Centralblatt f. d. Med. Wiss.," 1869, and Noel, "Etude général sur les gaz du Sang. Thése.," Paris, 1876.

§ See Trifanowski, Pflüger's "Archiv," Band ix 1874, p. 492, and Socoloff, idem., Band xii. 1875, p. 54.

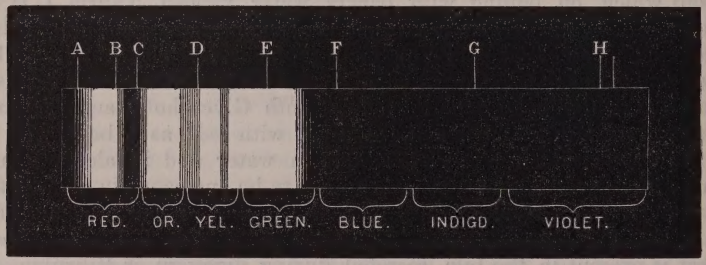
this acid bears to the glycocholic (which differs greatly in different animals) may be estimated by the amount of sulphur in the mixture of the two. The bile often contains copper. The *mucin* varies in quantity, and appears to be derived from the epithelial cells of the excretory ducts and gall-bladder, and not from the liver cells, since its quantity is lowest when the secretory activity of the organ is at its height. The *diastatic ferment* is small in quantity,* but has been found in the bile of the frog, pike, carp, goose, duck, chicken, sheep, ox, pig, rabbit, cat, and horse, and in Man. The most important constituents of the Bile are the salts of the biliary acids and the colouring matters. Gmelin found that on the addition of neutral acetate of lead to fresh ox gall, a resinous and crystalline acid was precipitated, to which he gave the name of cholic acid. Strecker determined the formula of cholic acid to be $C_{26}H_{43}NO_6$, and observed that when it was boiled with saturated baryta water, it takes up one eq. of water, and breaks up into Glycocol, $C_2H_5NO_2$, and Cholalic acid, $C_{24}H_{40}O_5$. Lehmann afterwards, to avoid confusion, termed the cholic acid of Gmelin Glycocholic acid, by which name it has since been recognised. Strecker further showed that ox gall contained another acid, which he termed choleinic acid, and which, on boiling with baryta water, yielded, Taurin, $C_2H_7NSO_3$, and cholalic acid, one eq. of water being at the same time taken up. Lehmann changed the name of Choleinic to Taurocholic acid. The acid of the bile of fish, serpents, and the sheep is chiefly, and of the dog almost exclusively, composed of Taurocholic acid. In man, both Glycocholic and Taurocholic acids are present in the bile, and are united with soda as a base, with which they form salts that are readily soluble in water and in alcohol, but are insoluble in ether. These two acids appear to be analogous in composition to Hippuric acid, and to be composed of Glycocoll or of Taurin combined with Cholalic acid.† The chief colouring matter of the bile, and almost the only one that is present in the bile secreted during digestion, is Bilirubin, which has a beautiful bluish-green colour, and is capable of being converted by oxidation into the second colouring matter which is chiefly present in the greenish bile secreted by cold-blooded animals, and by warm-blooded animals during the fasting state, and is named Biliverdin. Both are found in considerable quantity at the borders of the placenta in the dog, and probably in other animals, and bilirubin occurs as a pathological product in old extravasations of blood; Bilirubin is here sometimes seen in the form of small rhombohedral crystals, and constitutes the Hæmatoidin crystals of Virchow.

* Jacobson, "De Sacchari formatione," &c., Regimont, 1865; and Wittich, Pflüger's "Archiv," Band vi. p. 181, 1872.

† The precise chemical composition of cholalic acid is unknown, but is taken as $C_{24}H_{40}O_5$. It is not present in fresh bile nor in any tissue of the body. In the intestinal canal it is formed from the taurocholic acid, and is in part discharged with the fæces. It is easily soluble in alcohol, but dissolves with difficulty in ether, and not at all in water. From the ethereal solution it crystallizes in prisms, and from its solution in diluted alcohol in tetrahedra. When separated from the watery solution of one of its salts, it is precipitated in a tenacious resin-like state, which crystallizes readily on the addition of a little ether. It is not volatile. Baryta cholalate is soluble in 30 parts of cold, and in 23 parts of boiling water, which affords a means of distinguishing its salts from those of the fatty acids. All combinations of cholalic acid exhibit when in solution right-handed circumpolarization, in this respect differing from all other substances found in the body, with the exception of grape sugar and Glycogen. On being heated to 200° C. (392° F.), or on being boiled with strong hydrochloric acid, cholalic acid yields the anhydride, $C_{24}H_{36}O_3$, called also dyslysin. When boiled with dilute sulphuric or hydrochloric acid, an amorphous substance is formed, which has been named choloidinic acid, but which is only a mixture of cholalic acid and dyslysin. Heated to fusion with caustic alkali, dyslysin takes up water and again forms pure potash cholalate. The bile of the pig contains the glycocoll and taurin compounds of an acid allied to cholalic acid and named hyocholalic acid, $C_{25}H_{40}O_4$. The bile of the goose again contains the salts of another acid combined with taurin, named the chenocholalic acid, $C_{27}H_{44}O_4$.

Its composition is differently given as $C_{32}H_{36}N_4O_6$ (Städeler and Maly), and as $C_9H_9N_9O_2$ (Thudichum).* Various experiments tend to show that the biliary colouring matters are not formed exclusively in and by the Liver, but rather that they are in part preformed in the Blood, so quickly is their elimination from the body effected. It is remarkable that, notwithstanding the comparatively-minute proportion in which the cholesterin and colouring matter exists in ordinary bile, cholesterin should usually be the principal ingredient of the biliary concretions which are frequently found in the gall-bladder and bile-ducts; and that the bile-pigment with choloidinic acid and a calcareous base should also occasionally accumulate, so as to form solid masses which consist of little else. The fresh normal Bile of man, the cow, pig, and dog, exhibits no absorption bands, though these appear in the alcoholic extract when the bile has undergone change.† Dr. Dalton,‡ working with sheep's Bile, finds that the spectrum is very short, the light being totally absorbed at a considerable distance from the refrangible end, and that it terminates suddenly. It presents, as is shown in the accompanying diagram, three absorption-

Fig. 178.



Spectrum of green bile.

bands, one in the red at the situation of the line C, which appears to be due to the green rather than the red colouring matter of the bile.§ A second, much more faint and less constant in position, situated at the junction of the

* The nature of the colouring matters has not been very accurately determined—for Städeler (1863) isolated five distinct compounds: Bilifulvin, Biliverdin, Bilifuscin, Biliprasin, and Bilihumin; whilst Maly (1864, Bernard, 'Physiologie Générale,' "Revue Scientifique," 1873, p. 462) finds only one substance, Cholepyrrhin; and Dr. Thudichum (1872, "Clinical Physiology," 1872, p. 18), describes two, Cholophæin or Bilirubin, $C_9H_9NO_2$, and Bilifuscin, $C_9H_{11}NO_3$. The relationship of these colouring matters to the colouring matter of the Blood, first suggested by Virchow, ("Archiv f. Path. Anat.," Band i. 1848, p. 421) has been rendered probable by the discovery of Zenker ("Jahresbericht von der Gesellsch. f. Natur und Heilkunde in Dresden," 1858, p. 53) of crystals of Hæmatoidin in inspissated Bile, by the circumstance that both contain iron, and by the observation of Gübler ("Gaz. Méd. de Paris," 1859, p. 469) that Bilirubin and Hæmatin give the same play of colours with HNO_3, except that the green colour is most persistent in the former and the violet in the latter. R. Maly ("Centralblatt f. d. Med. Wiss.," 1871, p. 849, and "Annal. der Chemie u. Pharm." Band clxiii. p. 77, 1872) has pointed out that there is a close relation between Cholepyrrhin, or Bilirubin, and the colouring matter of the Urine obtained by Jaffe (Virchow's "Archiv," Band xlvii.), and named by him Urobilin, and with the colouring matter of the fæces obtained by Vanlair and Masius ("Centralblatt f. d. Med. Wiss.," 1871, p. 369). Feltz and Ritter (Robin's "Journal de l'Anatomie," 1875, p. 162), and Tarchanoff (Pflüger's "Archiv," 1874, Band ix. p. 329), have shown that if the colouring matters of the Bile or of the Blood are directly injected into the Blood, they are rapidly excreted in a more or less modified condition by the Urine.

† Foster, "Text Book of Physiology," 1878, p. 196.

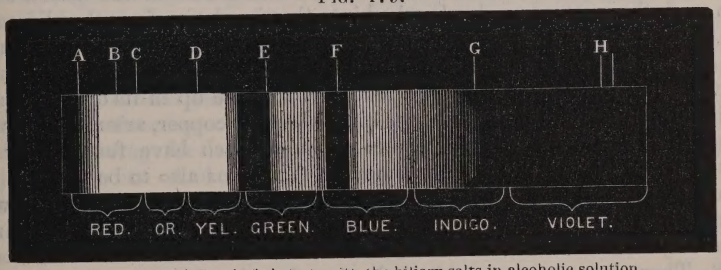
‡ "A Treatise on Human Physiology," 6th edit. 1876, p. 209.

§ On Vierordt's system of notation, in which the eight principal lines of the solar spectrum are taken as fixed points, A, B, C, D, E, F, G, and H, and the spaces between these considered as divided into 100 equal parts, the exact position of the band was in one case from B 20 C to C 10 D, and in another from B 13 C to C 18 D.

orange and yellow immediately to the left of the line D; and a third, which is very narrow, situated at about one-third the distance between D and E. The principal band at C corresponds very closely with the absorption-band of chlorophyll. As a rule, also, it presents a remarkable diminution in quality of the orange and red colours. Both Dalton and Schenk* obtained the spectrum (Fig. 179) from the purple fluid, resulting from the action of Pettenkofer's test on solutions of the taurocholate and glycocholate of Soda, exhibiting two wide and dark absorption-bands, one at E, extending from D 50 E, to E 25 F; the other at F, from E 60 F, to F 15 G, the spectrum terminating gradually about the line G. v. Wittich, in a case of biliary fistula in the human subject, found that the fresh bile contained a ferment capable of converting starch into sugar.† The index of refraction of bile for light was found by Valentin to be 1·3478; the specimen was not freed from mucus, and was taken from a subject several days after death.‡

347. We have now to inquire into the conditions under which the Secretion of Bile takes place; and one of the most important of these is the supply of

Fig. 179.



Spectrum of Pettenkofer's test, with the biliary salts in alcoholic solution.

Blood which the Liver receives. How far the blood supplied by the Hepatic Artery is the immediate source of the secretion has not been quite satisfactorily determined. Kottmeier§ and Küthe‖ found that no bile was secreted after ligature of this vessel, and they attribute the result to an alteration taking place in the nutrition of the cells destined to form the bile. Schiff, however, was unable to detect any diminution in a large dog upon which he had performed the same operation, and Röhrig¶ found the secretion was only slightly lessened. It is certain that the hepatic artery may indirectly furnish the supply of blood necessary for the secretion; for although, if the Vena Portæ be suddenly tied, the flow of bile is immediately stopped, and death ensues in the course of a few hours, yet if the obliteration be slowly effected, either by the gradual tightening of a ligature,** or, as occasionally happens, from disease, the secretion of bile still continues, though in diminished quantity and of more watery quality. In such instances it probably proceeds from the blood of the hepatic artery, the capillaries of which discharge themselves into the lobular plexus of veins, and in cases of malformation have been actually observed to pass into the ramifications of the umbilical vein, forming a plexus in the lobules that exactly resembled the ordinary portal plexus.†† Its

* "Anatom. Physiol. Unters.," Wien, 1873.

† Pflüger's "Archiv," 1872, Band vi. p. 181. Ranke, "Physiology," 1875, p. 287.

‡ Valentin, Pflüger's "Archiv," 1879, p. 84.

§ "Zur Kenntniss der Leber," Wurzburg, 1857.

‖ "Studien des Physiolog. Institut zu Amsterdam," 1861.

¶ Röhrig, Stricker's "Jahrbücher," 1873, p. 243.

** Oré, "Comptes Rendus," 1856, p. 463.

†† Such, at least, was found to be the case in the only instance in which the Liver was examined with sufficient care. See Kiernan, loc. cit.

secretion after such slow obliteration of the Venæ Portæ may also sometimes be due to the presence and enlargement of the accessory Venæ Portæ, which have been noticed by Sappey.* According to Bernard,† the engorgement of the Venæ Portæ consequent upon its slow obliteration is relieved by the presence of small anastomotic branches, with the Renal Vein corresponding to the Venous system of Jacobson found in the lower Vertebrata‡.—The fact that the secretion of Bile is normally formed, in great part at least, from *venous* blood, has been commonly connected with the hydrocarbonaceous nature of its chief components, which must exist (it is considered) in larger proportion in such blood than in that of the arteries. But it must be borne in mind that the urinary excretion, which is undoubtedly formed at the expense of the products of the disintegration of the tissues, is secreted from arterial blood; and since the bile is, as it were, the *complement* of the urine (the ultimate components of the two together making up the composition of blood), there seems no reason why arterial blood should not furnish its materials as abundantly (or nearly so) as venous. The real explanation of the peculiar relation of the Liver to the venous circulation is probably to be found in the action of the organ upon the matters newly absorbed into the circulation from the alimentary canal. That this action is not only assimilative, as already shown (CHAP. VI. Sect. 3), but is also to a certain extent depurative, appears from the fact that the liver tends to remove from the blood, and to store up in its own substance, certain foreign matters of an injurious kind—such as copper, arsenic, iron, manganese, lead, antimony, and potassium iodide—which have found their way into the tributaries of the portal system. This seems also to be the case with respect to pus, which, when taken-up from ulcers in the intestinal walls, is stopped in the liver, and not unfrequently gives rise to abscesses in its substance.§

348. There is strong reason for believing that the chief constituents of the Bile are elaborated in the liver itself, and are not preformed in the blood, since, although the tests for biliary acids are far more delicate than those employed for the detection of urea, no trace has been discovered of them in the blood of animals whose livers have been extirpated, though it might be expected that, if like the components of the urinary secretion, they pre-exist in the circulating current, and are merely eliminated from it by the action of the liver, they would accumulate in it when that elimination is checked by the removal of the secreting organ. Some of the constituents of this very complex secretion may undoubtedly be found in other organs or fluids of the body; thus, cholesterin is found in the blood, lymph, most glands, and abundantly in the brain. Taurin is a constant constituent of the lungs and muscles of many animals, and Taurocholic acid is stated by Cloez and Vulpian to exist in the supra-renal capsules. Glycocoll can easily be obtained from hippuric acid, which is constantly present in the urine; and even the colouring matters bilirubin and biliverdin occur normally in the placenta of the dog. Still there can be little doubt that the pigmentary substances and the conjugated tauro- and glyco-cholic acids are formed in the liver itself, and that they are produced at the expense of substances of an excrementitious character, whose retention in the circulating current would be injurious; this being strikingly demonstrated by the disturbance of the functions generally, and especially of

* "Gaz. Méd.," 1859, p. 489.

† "Leçons sur les Liquides de l'Organisme," 1859, vol. ii. p. 195.

‡ For other anastomotic branches, see Schiff in "Schweiz. Zeits. f. Heilkunde," Band i. 1862.

§ See Dr. G. Budd's "Treatise on Disease of the Liver," 2nd edit. chap. ii. sect. 1.

those of the Nervous system, which is consequent upon the suspension of the secreting process. When the suppression is complete, the powers of that system are speedily lowered (almost as by a narcotic poison), the patient suddenly becomes jaundiced, and death rapidly supervenes.* When the secretion is diminished, but not suspended, the same symptoms present themselves in a less aggravated form. The gall-bladder begins to contain bile at about the sixth month of intra-uterine life, and it has been shown by Simon and Frerichs that the *meconium* which is contained in the intestinal canal at birth is chiefly composed of inspissated bile; Kühne,† after referring to the results of various investigations, observes that the bile undergoes the same changes in the intestines as when boiled with acids or alkalies, or when allowed to putrefy. These changes commence in the lower part of the ileum, and are completed in the cæcum and colon. Glycocholic acid, which is decomposed with difficulty, may frequently be found in the fæces of animals, in which it constitutes the chief biliary acid, whilst in the fæces of Carnivora, whose bile is principally composed of Taurocholic acid, only cholalic acid appears. According to Bischoff, man discharges about 50 grains of the biliary acids by the fæces per diem, whilst Voit's estimate gives 170 grains as the quantity daily formed by the liver; 120 grains must, therefore be reabsorbed or otherwise disposed of.—The excrementitious character of the Biliary secretion is very strikingly indicated by its formation during fœtal life; which, as it can then have reference neither to the function of Digestion nor to that of Respiration, must be regarded as having for its purpose to free the blood of matter which would be injurious to it. And this matter can hardly arise from any other source than the 'waste' of the tissues (consequent upon the limited duration of their existence), which takes place even when the life of the organism is most purely vegetative.

349. From what components of the Blood the materials of the biliary secretion are immediately derived is a question that cannot yet be quite satisfactorily answered. The close resemblance in composition between the resinous acids of bile and the ordinary fats (especially olein), naturally suggests the idea that they are drawn from the fatty matters of the blood; an opinion which was supported by Lehmann on the grounds—first, of the diminished proportion of fat contained in the Hepatic as compared with the Portal Venous blood; secondly, of the increase in the quantity of bile observed after rich fat food; and, thirdly, of the emaciation which occurs in animals as a consequence of the formation of a biliary fistula, in spite of an abundant supply of albuminous food. It must be acknowledged, however, that there are various objections to this view, both physiological and chemical. Thus, it is maintained by Bidder and Schmidt that the flow of bile is not increased by a predominance of fat in the food, and that animals fed exclusively on fat do not secrete more bile than those entirely deprived of food: whilst it has been found by Nasse that it is to the presence of a large amount of albuminous compounds in the food that any great augmentation in the secretion is due.‡ Whatever may be their mode of origin, there is every reason to believe that the production of the components of bile is a necessary part of those processes of retrograde metamorphosis, by which the materials of the effete tissues are removed from the

* See Prof. Alison in "Edin. Med. and Surg. Journ.," vol. xliv.; and Dr. Budd, op. cit., chap. iii. Austin Flint ("Physiology of Man," vol. iii. p. 288, *et seq.*) has suggested that it is the cholesterin which acts as the poisonous agent, and has proposed the term 'cholesteræmia' for this form of blood-poisoning; but the observations of Feltz and Ritter (Robin's "Journal de l'Anatomie," 1875, p. 171) on the effects of the injection of cholesterin are opposed to Dr. Flint's view.

† "Physiol. Chemie," 1868, p. 103.

‡ See Prof. Lehmann's "Physiologische Chemie," 2nd edit., Band ii. pp. 64–66.

system. The increase of the secretion after each ordinary ingestion of food (§ 125), and its marked and progressive diminution in animals entirely deprived of aliment (as determined by MM. Bidder and Schmidt), indicate that the secretion takes place, in part at least, as a reflex act, occurring in response to the stimulation of the gastric and intestinal nerves; in part also to the absorption of digested aliment by the radicles of the Vena Portæ and its conduction to the liver; and, lastly, and perhaps chiefly, to the increased flow of blood to the organ which follows the ingestion of food.* The experiments and observations of Schiff,† Lussana,‡ and others have demonstrated that a constant circulation of bile takes place in healthy conditions, so that a large portion of that which has been secreted by the liver and discharged into the intestines is reabsorbed from thence and again separated by the liver. They found that on inserting a canula into the gall-bladder, after tying the ductus communis choledochus, the discharge of Bile was considerable for the space of half-an-hour, the liver during this period performing the part of a secreting as well as of an excreting organ, but rapid diminution then took place in the amount discharged from the canula, because Bile no longer entered, and could therefore no longer be absorbed from the intestine. When, however, Bile was injected into the blood, the quantity eliminated quickly underwent increase, though it again diminished when the additional quantity had been excreted.

350. In regard to the influence of the Nervous system on the secretion of Bile, the results of experiments are contradictory: thus, whilst Pflüger states that no effect is produced on the secretion—in regard to its quantity, at least—by section of the Pneumogastrics, Phrenics, Splanchnics, or Sympathetics, by destruction of the Cœliac Plexus, nor after destruction of all the nerves entering the Porta Hepatis, provided the supply of blood be not interfered with, Röhrig§ found that section of the splanchnics or of the spinal cord, either of which causes dilatation of the abdominal vessels, is followed by increased flow of Bile, whilst, on the contrary, reflex irritation of the cord, (as by stimulating a sensory nerve) by contracting the vessels, diminishes it. The reason of this is that the most important factor in the secretion of Bile is the rapidity of the circulation through the vessels of the abdominal viscera. Irritation of the Spinal Cord is without effect if the splanchnics have been previously divided.‖ In regard to the action of Medicines on the flow of Bile, the observations of Bennett, Rutherford, and Gamgee¶ have shown that Calomel, Corrosive sublimate, and Podophyllin augment the secretion of bile;

* A remarkable and hitherto unexplained circumstance is that bile obtained from the gall-bladder in man and the dog contains about 10 per cent. of solids, whilst bile obtained from biliary fistula in man only contains from 2·24 to 2·28 per cent. of solids, and in the dog usually only about 3 or 4, or rarely 6 per cent.

† Pflüger's "Archiv," 1870, p. 598. The observations of Rosenkranz ("Verhandlungen d. Phys. Med.-Gesellsch in Würzburg," Band xiii. 1879, p. 224) support the statements of Schiff, and show that the reabsorption of the biliary salts is rapid, being easily demonstrable within an hour. They are in opposition to the statement of Tappeiner ("Amtlicher Ber. der 50 Naturforscher Versammlung in München," p. 237), that Glycocholic acid is reabsorbed in the jejunum and ileum, whilst the taurocholic acid is only taken up in the ileum. Rosenkranz thinks, however, that but little of the absorbed salts reappear in the bile, they rather seem to disappear in the blood after having effected, or in the act of effecting, changes in the blood corpuscles which lead to the production of fresh biliary salts.

‡ Lussana, "Lo Sperimentale," t. xxix. p. 337. See also "Brit. Med. Journal," January 4, 1873. Röhrig, loc. cit. § Stricker's "Jahrbücher," 1873.

‖ See Heidenhain, "Centralblatt," 1867, p. 662, and 1868, p. 710; and Munk, Pflüger's "Archiv," Band viii. p. 151, who think that there is a primary increased flow of bile on irritation of the spinal cord, which is due to the contraction of the muscular fibres they believe to be present in the biliary ducts. ¶ "Brit. Med. Journ.," 1869, vol. i. p. 411.

and those of Rutherford and Vignal,* that the same effect is produced on the secretion in the dog by Aloes, Rhubarb, Colchicum, Iridin, Ipecacuanha, Colocynth, Phytolaccin, dilute nitro-hydrochloric acid, ammonium and sodium benzoate, sodium salicylate, and ammonium phosphate. The biliary secretion is not materially modified in quantity by Morphia, Alcohol, Calomel, or Potassium iodide. Violent purgation usually diminishes the secretion of bile, and many substances, as magnesium sulphate and scammony, are powerful stimulants of the intestinal glands, but have little action on the bile. Acetate of lead is one of the few substances that depress the secretory action of the liver.

351. But besides the secretion of Bile, it appears that another purpose is fulfilled by the Liver—the production of an amyloid substance termed Glycogen; and we shall now proceed to consider the chief facts which have been ascertained with reference to this so-called 'Glycogenic function of the Liver.' It had long been well known that Vegetables were capable of producing Starch and Sugar from the inorganic materials of their food, but the presence of a form of Starch—Cellulose—as a constituent of the animal body, in the test of one of the Tunicata announced by Dr. Schmidt, and corroborated by the observations of Löwig and Kölliker,† was considered to be only interesting because it destroyed what had till then been looked upon as one of the most important means of distinguishing the tissues of the animal from those of the plant. In 1848, however, Bernard‡ observed that, whilst the Blood of the system generally, and that of the Vena Portæ in particular, in an animal fed exclusively on meat, appeared to be destitute of Sugar, a very notable quantity could be detected in the blood of the Hepatic Vein and right heart—that is to say, in the blood which had passed through the Liver. The question which arose—whether the sugar was formed by, or was only stored up in, the liver—was answered by showing that after the liver had been thoroughly freed from blood by the injection of water into the portal vein, sugar was formed anew; and in the course of this investigation it was incidentally shown that the amount of sugar obtainable from the liver increases, within certain limits, with the time after death at which it is examined. He immediately inferred that a new function, the formation of Sugar, was to be attributed to the Liver; that the sugar so produced was thrown into the circulation, and then, by undergoing combustion, ministered to the maintenance of animal heat. He was supported in this view by the authority and analyses of Lehmann,§ who suggested that the Sugar might proceed from the decomposition of albuminous compounds, since there was a smaller quantity of albumin in Hepatic as compared with Portal Venous blood; and there were also good chemical grounds for supposing that albumin might split up into nitrogenous compounds, represented by the conjugated biliary acids (which also contain the sulphur), and into non-nitrogenous compounds represented by Starch, Glycogen, and Sugar. Schmidt (of Dorpat) conceived that the Sugar might result from the decomposition of the fatty substances; whilst Frerichs thought that the albuminous substances might break up into Glucose and Urea. Bernard|| himself, however, was disposed to consider that Bile and Sugar were produced in the Liver independently of one another; first, because the formation of Sugar was most active at a much earlier period after food than that of Bile; and, secondly, because in one of the Mollusca (Limax flava) he found that the liver

* "Transact. Roy. Soc. of Edin.," vol. xxix. † "Annales des Sciences Naturelles," 1846.
‡ "Archives Gén. de Médecine," and "Nouveau Fonction du Foie," 1853.
§ "Comptes Rendus de l'Acad. des Sciences," 1855, p. 587.
|| "Leçons," 1854–55, p. 93, *et seq.*, a view which has been supported on histological grounds by Accolas, Thesis, Strasbourg, 1867.

secreted sugar and bile alternately, the former during, the latter after, digestion. The observations of Bernard, from their novelty and interest, attracted the attention of many chemists and physiologists, and it was soon shown that sugar, though in comparatively small proportion, was frequently present in the blood of the general circulation, and of the Vena Portæ, as well as in that of the Hepatic vein. Thus, Chauveau* found in the arterial blood of a Horse, which had fasted for six days, 0·6 parts in 1000 of Sugar, and in the systemic venous blood, 0·5 parts in 1000. Colin also detected traces of Sugar in the Chyle and Lymph. Very careful investigations were soon made† to determine the proportion of Sugar in the Liver, and in the blood drawn from different parts of the body in animals under different circumstances, the general results of which appeared to be that sugar existed in the arterial blood of the Dog in the proportion of about 1·5 per 1000; in the Vena Cava inferior, below the renal veins, 0·54 per 1000; and in the Vena Cava inferior, above the diaphragm—*i.e.*, above the entrance of the Hepatic vein, 1·12 per 1000. In Herbivora, the quantity of Sugar in the blood of the Hepatic vein amounted to about 1 per 1000 during fasting, and from 2 to 6 per 1000 at a period of full digestion, whilst the mean quantity found in the liver substance was found to be from $\frac{1}{2}$ to $2\frac{1}{2}$ per cent. The much larger proportion of sugar obtained from the liver of herbivorous as compared with carnivorous animals, especially after a meal containing much amylaceous or saccharine material, naturally led to the supposition that these substances are derived from the aliment, and are merely deposited in the tissue of the liver; and we accordingly find Figuier‡ and Sanson§ arriving at the conclusion that vegetables alone are capable of producing starch, a part of which, when formed, is applied by the plant to the nutrition of its own tissues, whilst another part, stored up in cells, becomes subservient to the nutrition of Herbivorous animals. In these, again, a portion of the starch is consumed in the vital processes, whilst another portion is distributed to the tissues, being especially abundant in the liver; and to this source they believed the sugar contained in the blood of Carnivora was traceable. This view, however, became untenable when it was shown that in animals fed exclusively for months on ordinary butchers' meat, in which only traces of dextrin were present, the presence of sugar in the liver, though in much smaller quantity, could readily be demonstrated. In such cases it was obvious that the sugar could not be derived directly from the aliment, but must have been the result of metamorphoses taking place in the economy.

352. In the meanwhile Bernard, pursuing his investigations, was struck with the circumstance, that if the vessels of the Liver were thoroughly cleared of Sugar by the injection of water, a fresh supply of that substance could be obtained, after the lapse of a few hours, upon re-injection; showing not only that the production of sugar must be external to the vessels, and in the very substance of the organ itself, but also that it is capable of taking place quite independently of all vital action. From a consideration of these facts, he was led to inquire whether there might not be some substance formed by and pre-existent in the hepatic tissue, from the metamorphosis of which the sugar proceeded; and he, coincidentally with Hensen‖ and Pavey,¶ was soon suc-

* "Gaz. Med.," 1857, and "L'Union Méd.," 1857.

† By Dr. Harley, Poiseuille, Lefort ("Gaz. Méd.," 1858), and others.

‡ See "Gaz. Méd," "Gaz. Hebdomad.," and "Comptes Rendus," 1867.

§ "Journ. de la Physiol.," 1858, p. 244; 1859, p. 104.

‖ "Archiv f. Path. Anat.," Band xi. p. 395.

¶ "Guy's Hospital Reports," 1858, p. 291; 1859, p. 204; 1861, p. 197. "Phil. Trans.," 1860.

cessful in obtaining a peculiar substance possessing properties intermediate between those of starch and dextrin, and capable, under the action of ferments, of being readily converted into sugar, and of ultimately undergoing alcoholic or lactic acid fermentation. This substance was termed Glycogen by Bernard; Hepatin, or Amyloid substance, by Pavy; and Zo-amylin by Rouget. It exists in an amorphous state in the cells of the Liver, being especially abundant in those adjacent to the branches of the hepatic vein. It belongs to the group of colloidal or non-diffusible bodies (Pavy.) The great influence exercised by the nature of the food on its amount has been clearly shown by Dr. Pavy,* M'Donnell, and Tscherinoff.† Dr. Pavy found, on analysing the livers of dogs fed exclusively on animal diet, about 7 per cent. of amyloid substance; whilst in those fed on meat and sugar it amounted to 14·5 per cent.; and in those fed on vegetable diet alone to 17 per cent. In cases where animals were fed on starch and sugar, the livers were pale and pulpy. No amyloid substance was present in animals dying of starvation or wasting disease.‡ The amount of Glycogen in the Liver of those animals in which the tissue of the organ is compact is much less than in those in which it is loose. In the Horse, for example, it is at least three times less than in the Rabbit. In Fowls, Brücke found it might reach the high proportion of 12 per cent. of the total weight of the Liver. In rabbits submitted for several days prior to death to different dietaries, it has been found§ that cane, milk, and grape-sugar and starch always leads to an increased per-centage of amyloid substance in the Liver, in from six to eight hours after administration,‖ but no increase occurs after the administration of mannite, lichenin, inosit, gelatin, or fats;¶ this organ appearing to seize upon these substances and store them up, so that the sudden entry of a large quantity into the general circulation is prevented. If, however, a very considerable quantity of sugar be introduced into the stomach, especially if it be empty (as it commonly is in the dog), it is quickly absorbed, and though conveyed to the liver, this organ is unable to metamorphose the whole of it, and the portion which escapes entering the general circulation is discharged by the Kidneys, when the proportion exceeds 3 per cent. of the blood. The same quantity of Sugar may be disposed of without producing diabetes if it be ingested slowly, or when the stomach is full (as it commonly is in rabbits), and thus Bernard accounts for the differ-

* "Phil. Trans.," 1860, p. 604.

† "Sitz. d. k. Akad. zu Wien.," Band li. 1865, p. 412. See also Dock, Pflüger's "Archiv," Band v. p. 571.

‡ This is not in accordance with Bernard's experiments ("Revue Scient.," t. viii. 1872–73, p. 1155), who found glycogen to be constantly present, even after prolonged fasting. Dock states that when in consequence of inanition all glycogen had disappeared from the liver, the ingestion of sugar into the stomach caused the appearance of large quantities in the liver in the course of a few hours, but no such effect was produced in rabbits by the ingestion of albumin. See Tiegel, idem, Band vi. p. 249. The differences in the amount of glycogen found by different observers under apparently similar conditions may perhaps be due to the circumstance pointed out by v. Wittich ("Centralblatt f. d. Med. Wiss.," 1875, p. 117), that the formation of glycogen does not take place with equal energy in all parts of the liver, some producing it more abundantly than others. Seegen, Pflüger's "Archiv," Band xix. 1879, p. 122, has demonstrated that the sugar formed in the dead liver is grape-sugar. Finn ("Würzburg. Phys.-Med. Verhand. N. F.," Band xi. p. 92) finds that glycogen differs somewhat according to the nature of the food on which the animal is fed. Glycogen, from a diet of grape-sugar, rotated light 173°, levulose 168°, glycerin 160°, albumin 163°.

§ See Luchsinger, Pflüger's "Archiv," Band viii., and Salomon, Virchow's "Archiv," Band lxi. p. 352.

‖ Konjkoff, "Diss." Petersburgh, abstracted in "Centralblatt," 1876, p. 734.

¶ v. Mering, Pflüger's "Archiv," Band xiv. p. 274.

ence in regard to the appearance of Sugar in the urine after the administration of the same quantity to dogs and rabbits.* The explanation that may be afforded of this is, that when sugar or glycose is rapidly ingested, it traverses and is expelled from the system unchanged, but when introduced more slowly, the liver formed has time to act upon it, and convert it into Glycogen, which is stored up in the Liver. Although, as the foregoing experiments show, the amyloid substance is much more abundant in the livers of animals fed on starch and sugar, from which, therefore, it doubtless in part proceeds, it must not be overlooked that it is also present in animals confined to a pure meat diet; in which case it is probable that it proceeds from the disintegration of albuminous compounds into hydrocarbonaceous and nitrogenized substances,† or it may be derived from the glycogen present in the flesh, used as food. In granivorous and herbivorous animals, as in Fowls and Rabbits, the albuminous compounds do not appear to be well adapted for the production of glycogen. Thus Weiss‡ found only traces of Glycogen in the liver of fowls fed for a fortnight on flesh and fibrin, and Dock found none in rabbits fed with white of egg. The same conclusion may be drawn from the fact that the quantity of glycogen in the liver of animals starving to death, and when therefore they are living on animal diet, is greatly reduced. Very different times are required for all the glycogen to disappear from the liver as a result of fasting in animals of different species, and even in different animals of the same species. Thus Luchsinger§ found from 4—6 days elapsed before it was reduced to a minimum in rabbits, whilst others‖ give $2\frac{1}{2}$ to 3 days. In dogs it is absent after from 14—21 days. In frogs after 2 days. Yet in hybernating animals the liver, after protracted hybernation, still contains a large amount of glycogen.¶ In 1859, Bernard** detected the presence of amyloid substance in the placenta of ruminants—in which, or rather, as has been since shown, in patches of cells lying on the inner surface of the amnion—it exists in considerable quantities. Shortly afterwards, Rouget†† discovered it in various embryonic cellular tissues, as in the epithelium of the skin, and of the alimentary and genito-urinary mucous membranes. It is remarkable that it is not found in the liver till its histological development is completed, or until about the middle of intra-uterine existence. It is present, except after long fasting, in the muscles, the proportion amounting in rabbits and frogs to about 0·4 or 0·5 per cent.‡‡ It has also been found in the testis, in the lungs and kidneys§§ and in pus.‖‖ It is not found in the bones nor in the nerves, though Jaffe has observed the presence of an amyloid substance in the brain. Amyloid substance has been found also in the bodies of several invertebrate animals, as in the snail (Bernard),¶¶ tape and round worm,*** cockle, scallop,††† mussel, oyster;‡‡‡ and the yellow cells of Radiolaria, but in these instances it appears to have little ten-

* See Brunton, Lectures in "British Med. Journal," 1874, pp. 1, 39, and 221; and Schöpffer, "Archiv f. Experiment. Path.," 1873, i. p. 72.

† See Hoppe-Seyler, Pflüger's "Archiv," Band vii. p. 399. Salomon (Virchow's "Archiv," Band lxi. 1874, p. 352) has demonstrated clearly that glycogen is formed in the liver from gelatin as well as from albumin.

‡ "Sitzungsber. d. Wien. Akad.," Band lxvii. abth. 3.

§ "Dissert" Zurich, 1875.

‖ Salomon and Salkowski, "Centralblatt f. d. Med. Wiss.," 1876, p. 392.

¶ Aeby, "Archiv f. Experim. Pathol.," Band iii. p. 181.

** Brown-Séquard's "Journal de la Physiol.," 1859, p. 30.

†† Id. p. 83.

‡‡ M'Donnell, Pamphlet, O Nasse.

§§ Abeles, "Centralblatt f. d. Med. Wiss.," 1876, p. 84.

‖‖ Salomon, "Deutsch. Med. Wochensch," 1877, No. 8. Kühne.

¶¶ Bizio, "Comptes Rendus," lxii. p. 675.

*** M. Foster, "Proceedings of the Roy. Soc.," 1865, No. 79.

††† Chittenden, "Annal. d. Chem. u. Pharm.," clxxviii p. 266.

‡‡‡ Pavy, Op. cit., 1868, p. 77.

dency to become transformed into sugar. The "corpora amylacea" of Virchow, observed as pathological formations in the kidney, spleen, and other organs, and at one time considered to be identical with amyloid substance, differ from it essentially in containing nitrogen.*

353. After the presence of an amyloid material was shown to be constant in the liver, and to precede the formation of sugar, it was supposed that some *ferment* was requisite by which, either in the hepatic cells themselves, or after the absorption of the starch into the blood, its conversion into sugar could be rapidly effected. Many efforts were made to ascertain the source of this ferment; and the spleen, thymus, thyroid, supra-renal, salivary, and pancreatic glands were successively extirpated by Schiff,†, without, however, his being able to determine whether any of them were instrumental in its formation. Bernard,‡ Hensen, and Cohnheim§ maintain that the ferment is thrown down with the amyloid substance on the addition of alcohol to the cold aqueous infusion of the liver; that it can be obtained by the same process as that employed to isolate ptyalin, which it resembles in properties; that it is rendered inoperative by boiling; and, finally, that it is contained in ordinary arterial blood, and in the blood of the vena portæ, the addition of such blood to a solution of glycogen effecting its conversion into sugar. The necessity for the existence of this ferment has been rendered doubtful by the investigations of Dr. Pavy,‖ whose experiments have led him to the following conclusions:—1. That the liver normally and *during life*, whatever may have been the nature of the food, contains little or no sugar, but a considerable proportion of amyloid substance; since if it be removed from the body instantly after death, and subjected to the action of caustic or carbonated potash or soda, or of extreme cold, no saccharine reaction can be obtained, though the presence of the amyloid substance can easily be shown. 2. That, *during life*, there is under ordinary circumstances very little difference in the amount of sugar contained in different specimens of blood, whether withdrawn from the systemic arteries or veins, the portal vein, or (by means of a catheter introduced through the jugular vein)¶ from the right auricle; the latter, of course, containing a large proportion of hepatic venous blood: the quantity of sugar present in all instances being extremely small, and varying from 47 to 73-1000ths of a grain per cent. 3. That *during life*, therefore, very little amyloid substance is taken up by the blood in its passage through the liver, as indeed might be anticipated from its low power of dialysing through animal membranes. On the contrary, after death, frequently from various disturbing causes during life, such as violent muscular action or embarrassment of the respiration, a conversion of the amyloid substance into sugar takes place in the substance of the liver itself, and the sugar so formed then quickly appears in the blood, often to so great an extent as to occasion diabetes. Moderate heat promotes the post-mortem formation of sugar from glycogen. The liver of a rat contained 2 per cent. of glycose three hours after death, and 5·2 per cent. after twenty hours.** Dalton found 5 seconds after death 1·8 per 1000 of glycose in a specimen of liver, 15 minutes after death 6·8 per 1000, and an hour after 10·3 per 1000.

* See Dr. Pavy's Gulstonian Lectures for 1863.

† "Unters. üb. die Zuckerbildung der Leber," Wurzburg, 1859.

‡ "Revue Scientif.," 1873, Lect. xviii. See also v. Wittich, "Centralblatt," 1873, p. 365.

§ Virchow's "Archiv," Band xxvii. p. 241.

‖ See his work on "Diabetes," 1868. See Ritter, "Zeitschrift f. rat. Med.," Band xxiv. p. 65; Schiff, "Journal de l'Anatomie," Robin, 1866; M'Donnell, "Observations on the Functions of the Liver," 1865.

¶ See on this point also M'Donnell, "Proceedings of the Royal Irish Society," 1868.

** M. Fort, "Manual de Physiologie Humaine," 1880, p. 612, quoting from Schiff.

354. At a very early period of the history of the glycogenic function of the Liver, it was found that the formation of sugar could be influenced through *the nervous system*. Bernard, for instance, observed that when the floor of the fourth ventricle, between the origin of the Pneumogastric and Auditory nerves (see Fig. 180) was pricked with a needle,* so great an increase in the quantity of sugar generated was effected in the course of an hour that was discharged by the urine, a condition of diabetes, lasting at most for twenty-four hours, being established. If, however, the same point be pricked after the branches of the sympathetic to the liver, which chiefly proceed from the splanchnics, have been divided, or the liver be removed entirely, no diabetes occurs.† Nor does any diabetes follow pricking the floor of the fourth ventricle in winter frogs, or in animals kept long fasting, or which have been supplied with arsenious acid in their food, in all of which the liver is destitute of glycogen. Diabetes can be induced by irritation of the central extremity of the divided vagus and by stimulation of any part of the nerve centres between the optic thalamus and the sixth dorsal vertebra,‡ and also by section of the splanchnics,§ which led Schiff to admit a form of diabetes from stimation, and a diabetes from paralysis of the hepatic vaso-motor nerves. Eckhard found that section of the inferior cervical ganglion was always followed by marked diabetes, and he arrived at the conclusion that the effects of pricking the fourth ventricle were transmitted through the inferior cervical and the upper thoracic ganglia. Diabetes was produced by Pavy both after division of the sympathetic cord in the neck and of the sympathetic plexus accompanying the vertebral arteries. The cause of the diabetes in these instances is the paralysis of the vaso-motor nerves, similar to that produced by direct injury to their centres, as when the fourth ventricle is punctured, or possibly by reflex irritation, as when the Pneumogastrics are irritated and there is a consecutive dilatation of the branches of the hepatic artery, and a more rapid circulation of blood through the liver. The importance of the free circulation of the blood through the liver is shown by the fact that if the vena cava in a frog be tied just below the liver, the blood is diverted by anastomoses into the vena portæ, and the liver becomes greatly congested, the result of which is that sugar appears in the urine. The vaso-motor nerves for the liver arise for the most part from the vaso-motor centres in the medulla oblongata, and descending through the cord, leave this by means of fibres which

Fig. 180.

To show the position of the punctures which most readily produces glucosuria, the lobes of the cerebellum are separated; below are seen the restiform bodies, the divergence of which bound the apex of the calamus scriptorius and the fourth ventricle. The puncture p' produces glycosuria, the puncture p glycosuria with polyuria, and a puncture a little higher up than p, albuminuria.

* Though not, according to Dock, if the animal has been kept fasting for several days. Pflüger's "Archiv," vol. v. 1872, p. 583.

† Eckhard, "Beiträge zur Anatomie u. Physiologie," 1867, Band iv., and 1877, p. 70.

‡ Moos, "Archiv f. Wiss. Heilk.," Band iv., and Schiff.

§ Hensen, "Verhand. der Phys. Med. Ges. in Wurzburg," Band vii. See "Guy's Hosp. Rep.," 1856, p. 204; also Cyon and Aladoff, "Bulletin de l'Académie Impériale de St. Pétersbourg," t. viii. p. 91. Abstract in "Centralblatt," 1872, p. 152, and in Dr. Brunton's Lectures in "Brit. Med. Journ."

accompany the vertebral artery and enter the lower cervical ganglia. Thence they proceed contained in two fasciculi, one of which passes on each side of the subclavian artery, forming the annulus of Vieussens to the first thoracic ganglion, and so through the successive ganglia of the sympathetic to the splanchnics and to the cœliac ganglion, and finally along the hepatic vessels to the liver. The experiments of Eckhard* render it probable that in some instances the fibres descend through the cord to a lower level than that of the vertebral artery before they emerge to enter the splanchnics. As section of the hepatic vaso-motor nerves at any point between the fourth ventricle and the liver causes vaso-motor paralysis and increased flow of blood through the liver, such section ought to be always followed by glycosuria, but this is by no means the case, and a rational explanation of its non-occurrence has been given by Cyon and Aladoff to the effect that although the section does really produce vaso-motor paralysis of the vessels of the liver, yet that the current of blood is not materially increased, because the same section, if made high up, coincidentally paralyses the vessels of the abdominal viscera which, owing to their great size, imprison as it were a large quantity of the blood, and so prevent any material change in the quantity of blood passing through the hepatic vessels. It has been found by Mayer that when grape sugar is injected into the blood, and the cord is divided between the fifth and sixth cervical vertebræ, the formation of glycogen by the liver is materially diminished, though the sugar is retained in the blood and applied to tissue changes. When the section of the cord is made between the seventh cervical and first dorsal vertebræ, the formation of glycogen in the liver is augmented without any decrease in the quantity of sugar contained in the blood. Lastly, section of the cord between the second and third dorsal vertebræ causes decreased glycogen formation in the liver and reduces the quantity of sugar in the blood.† In regard to the influence of the Pneumogastrics on the secretion of sugar by the liver, it has been ascertained that section of one of these nerves in the neck, or the stimulation of the peripheral cut surface is without effect. Section of both pneumogastrics diminishes the production of sugar. If, however, the *upper* cut surface of one or both pneumogastrics be stimulated, sugar rapidly makes its appearance in the urine, which appears to be due to a reflex influence conducted centripetally by the nerve, and causing paralysis of the vaso-motor centre. The pneumogastrics are, therefore, the sensory centripetally running nerves of the liver, and it has been suggested by Bernard‡ that the sympathetic presides over the secretion of sugar, and the pneumogastric nerve transmits to it the stimulus of the air, or, in other words, the oxygen of the air normally induces the formation of sugar through the pneumogastric and sympathetic nerves. It may here be remarked that the close relationship of the secretion of bile with the formation of glycogen is demonstrated by the observations of Dr. Legg,§ who has shown that after ligature or complete obstruction of the Hepatic ducts, glycogen is no longer formed by the Liver, and that puncture of the fourth ventricle fails to produce diabetes.

355. The influence of medicinal agents upon the glycogenic function of the Liver has received but little attention, though various substances are known to be capable of inducing diabetes. Cozé|| found the proportion of sugar nearly doubled both in the liver and in arterial blood after the adminis-

* Eckhard, "Beiträge," Band vii. 1873, p. 19.

† Mayer, Pflüger's "Archiv," Band xvii. p. 164.

‡ See Lefort, "Manuel de Physiologie," 1880, p. 616.

§ "British Med. Journal," 1874, p. 646, vol. i., and "Archiv f. Experiment. Pathologie," Band ii. Heft 5. See also Kulz, Pflüger's "Archiv," Band xiii. pp. 267 and 460.

|| "Comptes Rendus," 1857.

tration of morphia. Pavy* observed well-marked diabetes in animals after the administration of phosphoric acid, and also after poisonous doses of strychnia, when the circulation was maintained by artificial respiration. Harley obtained the same result in himself after eating freely of asparagus. Certain poisons, as Curare,† cause considerable increase in the quantity of glycogen in the blood and in the muscles, and it has been suggested that this is attributable to the paralysed muscles being unable to utilise the sugar formed in the liver. On the other hand, no glycogen is contained in the liver of animals kept motionless by bandages, notwithstanding an abundant supply of grape sugar.‡ The excess of sugar after the use of curare is discharged by the urine. It is remarkable that a few hours after the injection of from 3-10 grammes of glycogen into the veins hæmaturia supervenes.§ Glycogen, therefore, appears to be a solvent for the blood corpuscles. Achroodextrin also makes its appearance in the urine. Ewald‖ observed diabetes in Rabbits after the subcutaneous injection of nitro-benzole. The administration of large doses of caustic potash, or of carbonate of soda, is stated by Dr. Pavy to prevent the occurrence of diabetes under circumstances in which it would otherwise have been induced. The proportion of Glycogen in the Liver is diminished after the administration of arsenic and of amyl-nitrite.¶ Diabetes may be produced by disturbance of the *respiratory process*. Thus, it occurs in the Asphyxia caused by poisoning with carbonic oxide gas (Schiff), and Harley observed it in animals under the influence of ether, chloroform, liquor ammoniæ, and methylated spirit.** Reynosa†† produced it by making animals respire the vapours of benzoin and acetoin, and found that it followed asphyxia, slowly produced by the inhalation of carbonic, hydrocyanic, and sulphuretted hydrogen gases. Disturbances in the *circulation* of the blood have been found to exert a very distinct influence on the amount of sugar that can be obtained from the Liver. Thus, Bernard‡‡ found that the liver of a dog contained 3·5 parts of sugar in every 1000 parts, but on removing the liver from the body, or on arresting the circulation through it, the amount rose in the course of five minutes to 8 parts, and after twenty-four hours to 32 parts per 1000. Schiff, again, found that retention of the blood or retardation of the blood-current in any part, such as ligature or compression of the larger vessels, will lead to diabetes. Tieffenbach, however, found that the amount of sugar was increased by arrest of the circulation through the aorta or vena portæ. The experiment made by Winogradoff,§§ and already referred to, shows conclusively that the sugar is formed directly or indirectly by the liver, for when diabetes has been produced by the puncture of the floor of the fourth ventricle or by curare, it at once ceases on ablation of the liver, and a similar conclusion may be arrived at by puncturing the fourth ventricle in an animal to which arsenic has been administered for some time, for this drug has been found to prevent the formation of glycogen in the liver; and in consequence of the absence of glycogen in the liver, sugar is not produced in sufficient quantity to lead to its elimination by the kidneys. Chandelon‖‖ found that, after ligature of one common iliac artery in rabbits, the muscles of the operated side presented, in from

* "Proceedings of the Royal Society," No. 35.
† Abeles, "Wien. Med. Jahrb.," 1877, p. 551.
‡ Cecil Schulz, "Centralblatt f. d. Med. Wiss.," 1878, p. 15.
§ Böhm and Hoffmann, "Archiv f. Experim. Path.," Band vii. p. 489.
‖ "Centralblatt," 1873, p. 819. ¶ Konjkoff, loc. cit.
** See "Proceed. of Roy. Soc.," 1860. †† "Annal. d. Sci. Nat.," 1855, p. 131.
‡‡ "Comptes Rendus," t. lxxxiv. p. 1201.
§§ "Archiv f. Pathol. Anat. u. Physiologie," Band xxiv. p. 600, 1862.
‖‖ Pflüger's "Archiv," Band xiii. p. 626.

17—24 hours after the operation, a diminution amounting to 37—77 per cent. in the quantity of glycogen they contain as compared with those of the sound side. After section of the sciatic nerve, on the contrary, there was an increase of from 5—172 per cent. Hence he thinks muscular action is attended with glycogen consumption. Yet it must be observed that muscles may perfectly preserve their vital properties when no trace of glycogen can be shown to be present in them;* hence this substance can scarcely constitute the direct source of their activity.

356. The use of the amyloid substance developed in the Liver is involved in the greatest obscurity. By the earlier observers it was thought that it was immediately reconverted into sugar, and undergoing combustion in its passage through the Lungs, became subservient to the maintenance of animal heat. Various arguments have, however, been justly urged by Dr. Pavy against this view, and he is himself disposed to regard its production as representing the first step of assimilation of the *starchy* and *saccharine* elements of our food; and as these elements are known to lead to the formation of fat, he thinks there are grounds for believing that amyloid substance occupies an intermediate position between the two. The process of assimilation, he believes, may go on to the production of fat in the liver, or it may be that it stops short at the formation of another principle which escapes from the liver, and is elsewhere transformed into fat, or into the resinoid matter of the bile. In accordance with this view are the researches of Tscherinoff, who, obtaining similar results to those of Dr. Pavy in regard to the amyloid substance, noticed also that the use of food containing much hydrocarbonaceous matter, as sugar, greatly increased the proportion of *fat* in the liver. Two theories have been advanced to explain why the amount of glycogen in the liver is increased after the use of the carbo-hydrates. On the one hand, it may be said that the carbo-hydrates are more or less completely converted into glycogen within the liver, and that they are stored up in that organ;† and, on the other, it is maintained that the carbo-hydrates being readily oxidizable seize upon the oxygen of the blood and spare the glycogen derived from some other source.‡ The probabilities seem in favour of the former view. In regard to the origin of glycogen from *oleaginous* compounds, the experiments of Bernard, M'Donnell, and Luchsinger with fat dietaries seemed to show that this diet is unfavourable to the formation of glycogen; and even Salomon, whose recent experiments§ are not quite in accordance with those of his predecessors, shows that the proportion of glycogen is very much less on a fat than upon a saccharine diet, and about half as much as upon a gelatin diet. The concordant results of Weiss, Luchsinger, and Salomon show that glycogen is abundantly formed when glycerin is either administered alone in a diluted state or given with the food. Experiments with soap diet have been undertaken by Salomon, but have not enabled him to determine whether the glycogen in neutral fat diet proceeds from the glycerin it contains. The circumstance that the blood which enters the Liver is rich in *fibrin* and *albumin*, whilst that which leaves it is poor in these materials, has led Dr. M'Donnell to suggest it as probable that these materials break up

* See Luchsinger, Pflüger's "Archiv," Band xviii. p. 475.

† See Pavy, loc. cit.; Tscherinow, loc. cit.; Dock, Pflüger's "Archiv," Band v. p. 57.

‡ Scheremetjewski (Ludwig's "Arbeiten," 1869, p. 154) and Weiss ("Sitz. d. Wien Akad.," Band lxvii. abth. 3) advocate this view, on the ground that after the administration of glycerin the proportion of glycogen in the liver is notably increased, glycerin being a substance not likely to be converted into glycogen. Both Kühne and Luchsinger (Pflüger's "Archiv," 1873, Band viii. p. 289) have shown that this is an assumption unwarranted by facts.

§ Virchow's "Archiv," Band lxi. 1874, p. 354.

into secondary hydrocarbonaceous compounds which are partly eliminated by the bile ducts and are partly stored up as glycogen; and into nitrogenous compounds which reunite with the hydrocarbonaceous amyloid substance, and leave the liver as a newly-formed protein compound, partly perhaps as globulin, and partly as a material resembling casein or albuminose. Dr. W. Ogle* subsequently advanced a similar view, holding that before leaving the liver glycogen unites with some albuminous compound which enters the blood and is transferred to the muscles, where it undergoes decomposition with lactic acid and myosin: the former by its combustion yields muscular force, the latter is returned to the circulation to become again the carrier of a fresh portion of glycogen. That this is its destination he thinks is supported by the fact that muscle naturally contains a not inconsiderable amount of glycogen, as well as by the circumstance that this disappears or is greatly reduced when this tissue is brought into action;† and, lastly, it is in harmony with the fact that glycogen is abundant in most of the tissues of the embryo in which but little muscular energy is expended.‡ Gaetghens,§ from experiments with phosphorus on dogs, in which large quantities of fat are formed in the Liver, rising sometimes to 11 per cent., apparently from the metamorphosis of albumen, observes that there is no increase in the amount of glycogen, and is consequently opposed to this view.‖ Taking, however, such information as we at present possess into consideration, we seem entitled to conclude that the Liver exerts a twofold action on the blood which is traversing its capillaries—an assimilative and a depurative. By its operation as an assimilating organ it helps to prepare histogenetic material for conversion into blood and solid tissue, in the course of which it is capable of *producing* and of *storing up* amylaceous and oleaginous material in its cells, both of which are capable of being called upon for the maintenance of muscular force and of animal heat; whilst by its depurative action it frees the blood from the protein compounds which are destined to undergo retrograde metamorphosis, as being either superfluous or effete. A portion of these is again, in all probability, applied to the production of amyloid substance and fat; whilst the remainder, containing the nitrogen and sulphur, though a waste product, is in the form of the bile made subservient to digestion, and the introduction of fresh material into the blood before its final discharge from the body.

3. *The Kidneys.—Secretion of Urine.*

357. The Kidneys are a secondary urinary apparatus, developed from the Wolffian or Excretory duct of the primordial kidney. They cannot be regarded as inferior in importance to the Liver, when considered merely as Excreting organs; but their function only consists in separating from the blood certain effete substances which are to be thrown-off from it, and has no direct connection with any of the nutritive operations concerned in the introduction of aliment into the system. The following are the points in the minute structure of these organs which are of most importance in their Physiological relations:¶—Their glandular and vascular elements are embedded in a stroma

* See "St. George's Hospital Reports," vol. iii. 1868, p. 149.

† See Wundt, "Physiologie," 1873, p. 348.

‡ See Weiss, "Wien. Akad. Ber.," lxiv. Heft. 2; also Flint, "Physiology," vol. iii. p. 315; Lusk, "New York Med. Journ.," July, 1870; Tyson, "Introductory Lecture delivered at Pennsylvania College, Nov. 7, 1870;" Senator, "Centralblatt," 1871, p. 623.

§ "Centralblatt," 1871, p. 623. ‖ See Huppert, "Centralblatt," 1869, p. 349.

¶ See especially Mr. Bowman's Memoir in the "Philosophical Transactions," 1842; also Goodsir in "Edinb. Monthly Journal," 1842; Gerlach, Bidder, and Kölliker in Müller's "Archiv," 1845; Toynbee in "Med. Chir. Trans.," 1846; Johnson in "Cyclop. of Anat. and Phys.," Art. 'Ren.;' Gairdner in "Edinb. Monthly Journal," 1848; and Kölliker,

composed of connective-tissue continuous with the deep layer of the same tissue covering the surface of the organ. It consists of long fusiform cells, or Inoblasts, which stretch inward to the pyramids, and give a general support to the other tissues. A section of the kidney shows that it consists of an external or *cortical* portion, and an internal striated, and usually darker, *medullary* portion. Of these two parts the cortical is by far the most vascular, and the plexus formed by the tubuli uriniferi seems here to come into the closest relation with that of the sanguiferous capillaries, so that it is probably the seat of the greater part of the process of secretion; whilst the medullary is principally composed of tubes, passing in a straight line from the cortical portion towards their point of entrance into the ureter. The tubuli uriniferi commence in dilatations, named Malpighian Capsules (*d*, Fig. 181; *a*, Fig. 183), and terminate, after joining in their course, with others on the apex of the pyramids. The length of a tubulus is estimated at two inches. The total number of Capsules is about 500,000 in each kidney, and about 1000 tubuli join to form one papillary duct. If the course of a tubule be followed from its commencement in the capsule of Malpighi, it is found in the first instance to form a short neck to the capsule (*a*, Fig. 183), this part being lined by dark granular flattened epithelium. The tube then widens (*e*, Fig. 181; *b*, Fig. 183), and, still lying in the cortical substance of the kidney, becomes exceedingly tortuous, and is lined by cubical epithelium. It now forms a remarkable loop running towards the apex of the pyramid (*ff*, *gg*, Fig. 181), and returning to the cortical sub-

Fig. 181.

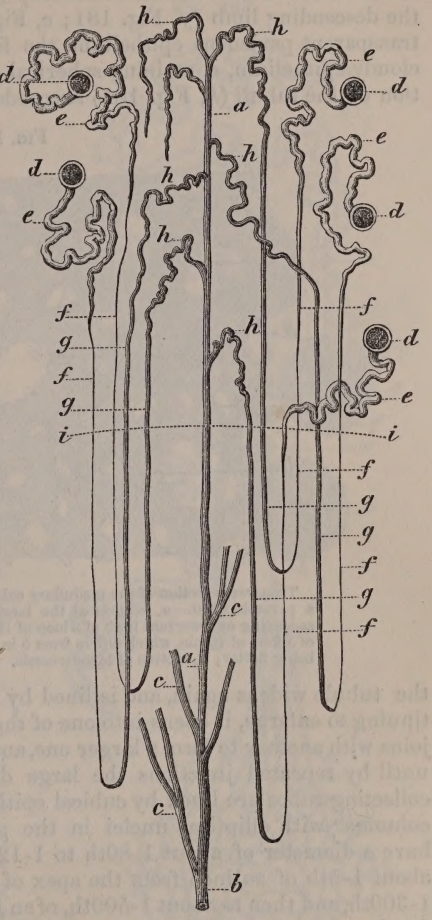
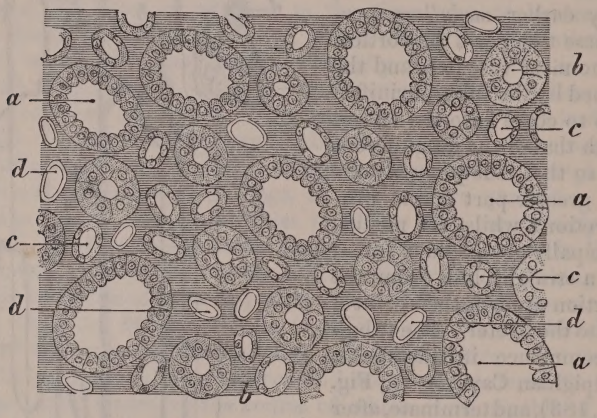


Diagram showing the course of the tubuli uriniferi.—*a*, straight tube, or tube of Bellini, or collecting tube running from the cortex of the kidney towards the papilla, where it opens; *b*, straight tube divided at a short distance from the apex of the papilla; *c*, *c*, other collecting tubes discharging their contents into *a*; *d*, capsule of Malpighi; *e*, tortuous portion of the tubules proceeding from the capsule, and forming the greater part of the cortical substance; *f*, delicate tubules, forming the descending limb of the loop of Henle; *g*, ascending limb of the loop of Henle; *h*, tortuous portion of the loop discharging itself into the collecting tubuli; *i*, *i*, line of demarcation between the cortical and medullary portion of the kidney.

"Mikroskopische Anatomie," and "Man. of Hum. Histol." (Sydenham Soc.); "Micros. Anat.," 1860; Isaacs, "Trans. N. Y. Acad. of Med.," vol. i. 1857; Henle, "Handbuch der Anatomie," Band ii. 1866; Hüfner, "Zur vergleich. Anat. u. Phys. d. Harncanälchen." Leipzig, 1866. Ludwig, Art. 'Kidney,' in Stricker's "Hum. and Comp. Histology," Syd. Soc. Transl., vol. ii. 1872, pp. 83–109; Frey's "Histology," translated by Barker, 1874. Krause, "Allgemeine Anatomie," 1876, p. 237. Toldt, "Geweblehre," 1877. Heidenhain, Schultze's "Archiv," Band x. Heft. 1. Pouchet and Tourneux, "Precis d'Histologie Humaine," 1878, p. 701.

stance. This loop was first recognised by Henle, after whom it has been named "the loop of Henle." It is throughout narrower than the tortuous portion, but the recurrent limb of the loop (*g*, Fig. 181; *b*, Fig. 182) is wider than the descending limb (*f*, Fig. 181; *c*, Fig. 182). The latter portion is lined by transparent pavement epithelium, the former by thicker, more granular, and cloudy epithelium, containing spherical nuclei. A short, rather tortuous portion of the tubuli (*h*, Fig. 181) succeeds, named the connecting canal.* Here

Fig. 182.



Transverse section of the medullary substance of the kidney near the base of a pyramid × 350.—*a*, section of the large collecting tubes; *b*, section of the ascending or recurrent limb of a loop of Henle; *c*, section of the descending limb of a loop of Henle, which differs from *b* in being smaller, and by its epithelium being flatter; *d*, section of blood-vessels.

the tubule widens again, and is lined by transparent cubical epithelium; continuing to enlarge, it opens into one of the collecting tubes (*a*, Fig. 181), which joins with another to form a larger one, and then again with another (*c*, Fig. 181), until by repeated junctions the large ducts of the papillæ are formed. The collecting tubes are lined by cubical epithelium, which gradually become more columnar with elliptical nuclei in the papillary tubes. The papillary ducts have a diameter of about 1-80th to 1-125th of an inch, but, at a distance of about 1-5th of an inch from the apex of the pyramid, they diminish to about 1-300th, and then to about 1-500th, of an inch, which diameter is nearly constant for the collecting tubes. In the papillæ themselves the ducts lose their basement-membrane, and are composed of the cells alone.† On examining one of the Corpora Malpighiana (*a*, Fig. 183) with a high magnifying power, it is found to consist of a convoluted mass of minute blood-vessels (Fig. 183 *e*), named the *glomerulus*, included in a flask-like dilatation of one of the tubuli uriniferi (Fig. 183 *f*). According to Mr. Bowman, this dilatation proceeds only from the termination of the tubule; and this seems to be usually the case, although it appears not improbable that it may sometimes be a lateral diverticulum, as described by Gerlach (loc. cit.). The inner surface of the Malpighian Capsule is lined by a layer of flat epithelium, the cells of which are distinct in both the adult and the fœtus. A similar layer covers the glomerulus, which is distinct in the fœtus, but only recognisable as scattered polygonal-nucleated

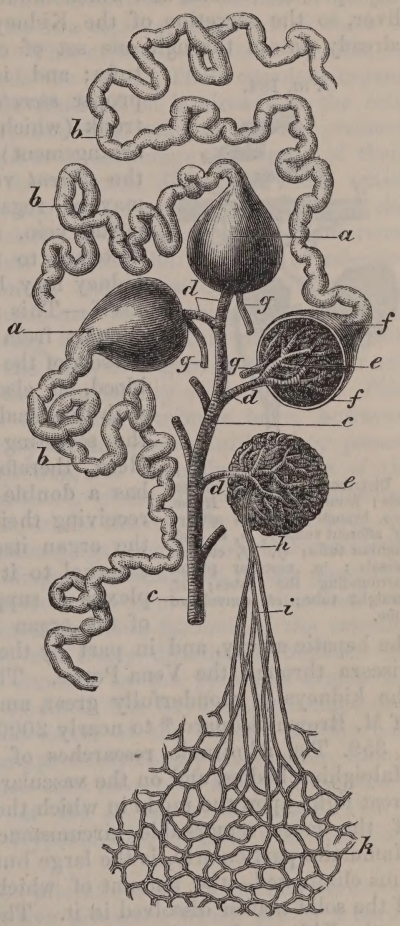
* Also intercalated or secondarily tortuous portion.

† See Heidenhain, "Archiv f. Microscop. Anat.," Band x.; also v. Seng, "Sitz. d. k. Akad. zu Wien.," p. 354.

cells in the adult.* The cells of the neck of the Capsule are furnished with cilia in the Frog and other Reptiles, and may be seen for many hours after death, in very active motion, directing a current down the tube (Hüfner, Mecznikow).

358. The Circulation of Blood through the Kidney presents a very remarkable peculiarity. The supply is derived in man (as in other Mammalia) direct from the *arterial* system; though in Fishes and Reptiles the urinary apparatus is connected, like the biliary, with the *portal venous* system, and even in Birds a portion of its blood is derived from the latter. But although this organ is supplied from the Renal Artery, yet it is not to its proper secretory apparatus that the blood of the artery is distributed in the first instance; for, on entering the kidney, this vessel speedily and entirely divides itself into minute twigs, which are the *afferent* vessels of the Malpighian (Figs. 183, *d*, 184, *a f*). After it has pierced the capsule, each twig dilates, and suddenly divides into two or three short twigs, which subdivide generally into more minute branches, terminating in from twenty to twenty-eight convoluted capillaries, which are collected in the form of a ball (Figs. 183, 184); from the interior of the ball, the solitary *efferent* vessel arises, which passes out of the capsule by the side of the single afferent vessel.† The *efferent* vessels on leaving the Malpighian bodies, separately enter the plexus of Capillaries (Figs. 183, *i*, 184, *p*) surrounding the tortuous portion of the tubuli uriniferi, supplying it with blood; from this plexus the renal vein arises.‡ Thus, there is a striking analogy between the mode in which the tubuli uriniferi are supplied with blood, for the purpose of elaborating their

Fig. 183.



Glomeruli of the kidney with the origin of the tubuli uriniferi.—*a*, *a*, capsules of Malpighi, enclosing the glomeruli; *b*, contorted portion of the tubuli; *c*, straight or interlobular arteries; *d*, afferent vessels, conveying blood to the Malpighian corpuscles; *e*, glomeruli formed by the ramification of the afferent arteries; *f*, capsule from which a portion has been removed to show the glomerulus within it; *g*, efferent vessels; *h*, efferent vessels, the divisions of which *i* break up into the capillary network *k*, of the kidney.

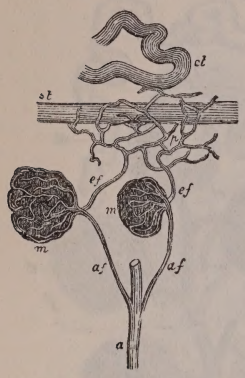
* Kölliker, "Man. Mic. Anat.," 1860, p. 408. Isaacs, "Trans. of N. Y. Acad. Med.," vol. i. 1857.

† Drasch ("Wiener. Akad. Sitz.-ber.," lxxvi. p. 79) maintains that there are two forms of glomeruli in the kidney, one near the surface with a non-nucleated capsule, the other near the medullary portion of the kidney with a nucleated capsule. The efferent vessel breaks up into the capillary plexus in the former, but runs into the arteriolæ rectæ in the latter.

‡ The reader will find a good summary of the opinions held by Virchow, Ludwig, and others on the course of the vessels, by Dr. Reg. Southey, in the first volume of the "St. Bartholomew Hosp. Reports," p. 177.

secretion, and the plan on which the hepatic circulation is carried on. For as the secretion of the Liver is formed from blood conveyed to it by one large vessel, the portal vein, which has collected it from the venous capillaries of the chylopoietic viscera, and which subdivides again to distribute it through the liver, so the secretion of the Kidney is elaborated from blood which has already passed through one set of capillary vessels, those of the Malpighian tufts; and is then collected and conveyed to the proper *secreting* surface; not, however by one large trunk (which would have been a very inconvenient arrangement), but by a multitude of small ones, the *efferent* vessels of the Malpighian bodies, which may be regarded as collectively representing the portal vein, since they convey the blood from the systemic to the secreting capillaries. Hence the kidney may be said to have a *portal* system within itself.—This ingenious view of Mr. Bowman finds support from the fact, that in Reptiles the *efferent* vessels of the Malpighian bodies (which receive their blood, as elsewhere, from the renal artery) unite with the renal branches of the Vena Portæ, to form the secreting plexus around the tubuli uriniferi. Here, therefore, the blood of the secreting plexus has a double source, the vessels which supply it receiving their blood in part from the capillaries of the organ itself, and in part from those of viscera external to it; just as, in the Liver, the secreting plexus is supplied in part by the nutritive capillaries of the organ itself, which receive their blood from the hepatic artery, and in part by the blood conveyed from the chylopoietic viscera through the Vena Portæ. The absolute quantity of blood traversing the kidneys is wonderfully great, amounting, according to the calculations of M. Brown-Séquard,* to nearly 2000 lbs. per diem.

FIG. 184.



Distribution of the Renal vessels; from *Kidneys of Horse.* —*a*, branch of Renal artery; *af*, afferent vessels; *m*, *m*, Malpighian tufts; *ef*, *ef*, efferent vessels; *p*, vascular plexus surrounding the tubes; *st*, straight tube; *et*, convoluted tube.

359. The admirable researches of Mr. Bowman on the structure of the Malpighian bodies, and on the vascular apparatus of the Kidney, have thrown great light upon the mode in which the Urinary secretion is elaborated. One of the most remarkable circumstances attending this excretion, in the Mammalia particularly, is the large but variable quantity of *water*, which is thus eliminated—the amount of which bears no constant proportion to that of the solid matter dissolved in it. The quantity of water which is passed off by the Kidneys depends in part upon that exhaled by the Skin, being greatest when this is least, and *vice versâ*: but the quantity of solid matter to be conveyed away in the secretion has little to do with this, being dependent upon the amount of *waste* in the system, and upon the quantity of surplus azotized aliment which has to be discharged through this channel.—The Kidney contains two very distinct provisions for these purposes. The *cells* lining the tubuli uriniferi are probably here, as elsewhere, the instruments by which the *solid* matter of the secretion is eliminated; while it can scarcely be doubted, that the chief office of the Corpora Malpighiana is to allow the transudation of the superflous fluid though the thin-walled capillaries of which they are composed. "It would, indeed," Mr. Bowman remarks,† "be difficult to conceive a disposition of parts more calculated to favour the escape of water from the blood, than that of the Malpighian body. A large artery

* "Journ de la Physiol.," 1858, t. i. p. 305.

† Loc. cit., p. 75.

breaks up in a very direct manner into a number of minute branches; each of which suddenly opens into an assemblage of vessels of far greater aggregate capacity than itself, and from which there is but one narrow exit. Hence must arise a very abrupt retardation in the velocity of the current of blood." The vessels in which this delay occurs lie in a capsule, from which there is but one outlet, the orifice of the tube. "This orifice is encircled by cilia, in active motion, directing a current towards the tube. These exquisite organs must not only serve to carry forward the fluid which is already in the cell, and in which the vascular tuft is bathed; but must tend to remove pressure from the free surface of the vessels, and so to encourage the escape of their more fluid contents."—Here we see the essential difference which exists between the *vital* agency concerned in the true Secreting process, and the *physical* power which occasions fluid exhalation or transudation. This difference is precisely the same as that which exists between the *vital* act of selective absorption, and the *physical* operation of endosmose or imbibition. By Imbibition and Transudation, certain fluids may pass through organic membranes, in the dead as well as in the living body; and this passage depends merely upon the physical condition of the part, in regard to the amount and the nature of the fluid it contains, and the permeability of its tissues.* That the epithelium of the several parts of the urinary tubules have, however, different functions is rendered probable by the different affinities they possess for staining agents,† after carmine injection, for example, the cells of the surface of the glomeruli becoming reddened, whilst those of the contorted portion of the tubuli remain colourless, whilst the opposite obtains with the sulphindigotate of soda. Other observations‡ again tend to show that albumin when present in the urine is chiefly or altogether eliminated by the glomeruli. The *lymphatics* of the Kidney are divided into two sets, a superficial and deep, the former arise amongst the connective tissue fasciculi of the capsule; the latter accompany the arteries, and are freely distributed between the tubules of the cortical part. They descend in the pyramids beside the *arteriolæ* and *venæ rectæ*, and issue at the hilus, but have many communications also with the superficial set. The *nerves* of the Kidney contain both pale and doubly contoured fibres, and are probably chiefly vaso-motor, though some must be sensory. A few ganglion cells have been found in the tubes.§ To chemical investigation the tissue of the kidney yields Inosit, Taurin, Leucin, Tyrosin, Kreatin, Xanthin, Hypoxanthin, Cystin, and sometimes Urea and Uric Acid.

360. The Kidney is liable to undergo alterations of its normal structure, from a perversion of its ordinary formative processes, which are of a nature very analogous to those occurring in the Liver, though with differences arising out of the peculiarities of its conformation.‖ Several different kinds, as well as degrees, of such alteration, have been described (as it now appears) under the general term "Bright's disease," which has been applied almost indiscriminately to almost every kind of chronic disease of the structure of the Kidney, whether produced by congestion, inflammation, or fatty degeneration, that is attended with the presence of Albumin in the Urine. As has been already

* See Lionel Beale, "Kidney Diseases," &c., 1869, p. 17; Tyson, "American Journal of Medical Sciences," 1869, p. 395; "Lancet," vol. i. 1870, p. 57.

† See Heidenhain, Schultze's "Archiv f. Mic. Anat.," Band x.; v. Wittich, ibid. Band xi. p. 75. ‡ Nüssbaum, Pflüger's "Archiv," Band xvii., 1878, p. 584.

§ Krause, "Allgemeine Anatomie," 1876, p. 245; Loc. cit., p. 75.

‖ For full accounts of the pathological conditions of the Kidneys and of the Urine in "Bright's disease," the reader is referred to the recent works of Drs. Basham, Johnson, Dickinson, and Beale.

stated (§ 140) of the albuminous substances taken up from the alimentary canal, a portion is directly absorbed in the form of albumin, whilst a portion is converted before absorption into peptones. According to Fick,* it is only the albumin which is directly absorbed that is applied to the reparation of the tissues and the formation of the albuminoids of the organism. The peptones, on the other hand, after their entry into the blood, undergo decomposition into urea and non-azotized products, which last may be applied as oxidizable materials to the performance of muscular work and the generation of heat. It is certain that if peptones be injected into the veins of an animal, the whole of the nitrogen they contain appears, in the course of a few hours, in the urine, whilst, if the kidneys have been previously extirpated, the quantity of urea which accumulates in the blood is much greater than after simple extirpation without injection of peptones, or even, after extirpation, with injection of albumin into the veins. Fick specially insists on the great increase of urea that occurs shortly after food has been taken as an evidence that the peptones are rapidly decomposed after absorption. It must be admitted, however, that when large quantities of raw albumin are consumed, a portion is discharged by the kidneys as a foreign substance, and that some kind of assimilating action is probably undergone by all forms of albumin before their entry into the blood;† and it is probably, in part at least, to the want of such assimilation of the newly-absorbed albumin, that we are to attribute the increase of albumin in the urine passed soon after meals, by patients suffering under Bright's disease; something, however, may be due to the simple augmentation of the bulk of the blood, and especially of its solids. But, again, any cause which augments the general blood-pressure, or which produces congestion of the vessels of the kidney, favours the passage of the ordinary albumin of the blood into the urine;‡ and thus we see how albuminous urine may be produced by pregnancy, in which condition the total quantity of blood is increased; by cold, owing to the repulsion of blood from the cutaneous surface to the kidney, by the exciting influence of cantharides or other irritant diuretics, or by any obstruction to the return of blood from the capillary plexus by the renal veins.§

* See Beaunis "Nouveaux Éléments de Physiologie Humaine," 1876, p. 515.

† See Hammond ("Experimental Researches," Philad. 1857, p. 31), who found on restricting himself to a purely albuminous diet, that his urine first contained a great excess of urea, and on the eighth day albumin made its appearance. Bernard also observed its presence in his urine after eating six eggs fasting ("Leçons," 1859, vol. ii. p. 138), and Mr. D'A. Power obtained it after an exclusive diet of eggs for three days.

‡ See Robinson in "Med.-Chir. Transact.," vol. xxvi. p. 51.

§ Magendie, indeed, found that the mere injection of about a pint of water into the veins of a large dog was sufficient to cause the urine quickly to become albuminous, the effect remaining for 10 or 12 hours (Bernard, "Leçons," 1859, vol. ii. p. 139). Overbeck ("Sitzungsbericht: d. k. Akad. d. Wiss. zu Wien," 1863, p. 189) has also made the curious observation that compression of the renal *arteries*, whilst it rapidly diminishes the quantity of urine and of urea secreted, also occasions the discharge of albumin in the urine; though if at the same time a ligature be applied to the ureters, the appearance of albumen is completely prevented. Albuminous urine has been observed in certain forms of heart-disease (Rayer), and after certain lesions of the nervous system, as intra-cranial section of the fifth pair of nerves (Longet, "Physiologie," p. 952), and section of the cerebral peduncles (Schiff); also in scarlet fever, measles, small-pox, erysipelas, pyæmia, typhus, typhoid, rheumatic and malarial fevers, cholera, purpura, scurvy, diabetes, syphilis, certain forms of pneumonia, pregnancy, post-parturient conditions, gout, chronic alcoholism, dyspepsia from excessive eating, and in mollities ossium. See G. Johnson, "British Med. Journal," January 11th, 1873. It has been shown by Brown-Séquard, Schiff, and other experimenters, and especially by Ollivier ("Archives Générales de Méd.," Feb., 1874) that both puncture of the floor of the fourth ventricle, and hæmorrhage into the substance of the hemispheres, is attended with great congestion of the kidneys, and albuminuria, but whether, as Schiff thinks, this is due to paralysis of the vaso-motor nerves, or, as Brown-Séquard thinks, from spasm of the veins,

361. The nature and purposes of the Urinary secretion, and the alterations which it is liable to undergo in various conditions of the system, are much better understood than are those of the Bile: this is owing, in great part, to the two circumstances, that it may be readily collected in a state of purity, and that its ingredients are of such a nature as to be easily and definitely separated from each other by simple chemical means. There can be no doubt that the chief purpose of this excretion is to remove from the system the effete *azotized* matters, which the blood takes up in the course of its circulation, or which may have been produced by changes occurring in itself. This is evident from the large proportion of Nitrogen in the solid matter dissolved in the urine; and from the crystalline form presented by much of this solid matter when separated, a form which indicates that its state of combination is such as to prevent it from conducing to the nutrition of the system. The injurious effects of the retention of the components of the Urinary secretion in the Blood are fully demonstrated by the results of its cessation; whether this be made to take place experimentally (as by tying the renal artery), or be the consequence of a disordered condition of the kidney. The symptoms of *Uræmia* (as this condition has been appropriately termed) are altogether such as indicate the action of a specific poison upon the Nervous system; affecting either the Brain or the Spinal Cord, separately or both together. These effects have been attributed by Frerichs and others* to the conversion of urea in the blood into carbonate of ammonia, and in a case recorded by Spiegelberg not only was the quantity of urea in the urine greatly diminished, but the proportion of this substance in the blood was augmented to three times its normal amount, whilst clear evidence was obtained by Dr. Gscheidlen that the blood contained a considerable excess of ammonia. Experiments on animals in which carbonate of ammonia has been injected into their veins show that conditions analogous to the uræmic state can be established, the animals first becoming restless and then exhibiting both tonic and clonic spasms, and finally passing into a state of deep coma.† Other views again are‡ that the suppression of the urinary secretion prevents the discharge

or of the veins and arteries, leading to engorgement and rupture of the capillaries, cannot at present be stated with certainty.

* See Babington, "Guy's Hosp. Rep.," 1836, p. 360; Owen Rees, "On the Nature and Treatment of Diseases of the Kidney," 1850; Frerichs "Die Brightshe Krankheit," 1851; Spiegelberg, "Archives of Gynæcology," 1870, and Hämpeln, "Dorpat Med. Zeits.," Band iv. 1873, and "Lond. Med. Record," vol. i. 1873, p. 611.

† Voit (Henle and Meissner's "Bericht," 1867, p. 358) is inclined from his experiments to hold that the effects observed in uræmic poisoning are due to the action of the various secondary compounds and alkaline salts proceeding from the disintegration of the albuminous constituents of the body which are retained in the blood in this disease upon the *central* parts of the nervous system, no ammonia being generated except on the intestinal mucous membrane. (See also G. Johnson, "Brit. Med. Journal," vol. i. 1873, p. 192); Mantegazza ("Centralblatt," 1870, p. 576), on the other hand, finding that intravenous injection of urea or of urine produces convulsions both in curarized frogs and even in muscles excised from the body, regards the action as peripheric, and not centric. Traube attributes the symptoms of uræmic poisoning to too great fluidity of the blood, and over-tension of the systemic vessels leading to œdema and anæmia of the brain; but Picot's experiments ("Comptes Rendus," July 6, 1874), in which water was injected at considerable pressure, are opposed to this view. Rosenstein (Virchow's "Archiv," Band lvi. 1872, p. 383), Oppler, and others contend that the symptoms caused by the injection of ammonia differ essentially from those of uræmic poisoning. Urea ingested by the stomach is eliminated unchanged. See Rabuteau in "L'Union Médicale," 1872, No. 142. For an account of the effects of the injection of ammonia into the circulation, see Tibbits, "Med. Times and Gazette," 1872, No. 1166. The whole subject is fully discussed in Bartel's work on 'Diseases of the Kidney' in Ziemssen's "Cyclop.," Amer. Edition, translated by Southey, vol. xv., 1877, p. 109, *et seq.*

‡ Rommeläre, "Journal de Médicine," vol. xliv. and xlv. 1867.

of effete products or the elaboration of albuminoid substance throughout the entire organism, if Nature does not provide some other vicarious mode of supplementing this excretion. Urea is one of the last steps or stages of the metamorphosis of these albuminoid substances, and, when urea accumulates in the blood, it may change the character of this fluid, and consequently the vital (nutritional) processes in various parts of the body. The entire work of transforming the albuminoid substances is arrested, so that we have to deal with the retention in the system, not merely of urea, but also of nitrogenous substances in all the different stages of oxidation through which they pass within the organism.

362. In order to form a correct opinion of the state of the Urinary secretion in morbid conditions of the system, it is desirable to be acquainted with every leading particular regarding its normal character.—Fresh healthy Urine is a perfectly transparent, amber, yellow-coloured liquid, exhaling a peculiar but not disagreeable odour, having a bitterish saline taste, and containing about 1–20th of its weight of solid constituents. The index of refraction for light of fresh morning urine, sp. gr. 1·0206 at 16° C. was found by Valentin to be 1·3395, but it may rise to 1·3443.* It is less when the urine contains albumin, higher when it contains sugar. The only morphological elements which it normally contains are pavement epithelium cells and mucous corpuscles from the lining of the urinary passages; which, however, are present in healthy urine to only a very small amount. But in certain morbid states of the urine, minute cylindrical bodies are seen in greater or less abundance, which are obviously derived from the tubuli uriniferi; these are sometimes composed almost exclusively of the epithelial lining of the tubes, of which the cells remain adherent to each other, notwithstanding their detachment from the basement membrane beneath; whilst sometimes they are fibrinous moulds of the interior of the tubes, formed by exudation of granular plastic material, and containing blood or pus-corpuscles; whilst in other instances, again, they are perfectly transparent, or hyaline, and are then believed by Dr. Basham to correspond to the viscid mucous exudations poured out from all inflamed mucous surfaces. The first of these forms occurs chiefly in desquamative irritation of the kidneys; the second, as a consequence of acute inflammation, and the last, in the advanced stages of "Bright's disease," as well as in the gouty and atrophic kidney.†—In all natural conditions of the Human system (even when a vegetable diet is used, though it may then become neutral) the urine possesses a well-marked acid reaction. When it is left to itself for some time, slight nebulæ, consisting of mucus, are formed in it; and these gradually fall to the bottom. Soon afterwards an unpleasant odour is developed; instead of an acid, an alkaline reaction is presented, in consequence of the decomposition of the urea into carbonate of ammonia; and a precipitation of earthy phosphates then takes place. A turbidity may be produced, however, by the precipitation of urates of soda and ammonia, on the simple cooling of the urine, without any such departure from its normal composition as would probably constitute disease, but under some of the conditions hereafter to be specified. But if the urine be turbid when it has first passed from the body, and has a temperature of 98° or 100°, it must be considered as abnormal.

363. *Quantity.*—Dr. Parkes,‡ who has collected the averages of many

* Pflüger's "Archiv," 1879, p. 85, Band xix.

† See, for drawings and descriptions of these, the work on "Renal Dropsy," by W. R. Basham, M D., 1866.

‡ "On the Urine," p. 5.

different observers, states that 52½ fluid ounces may be considered to represent the mean quantity of urine discharged in 24 hours by healthy male adults between 20 and 40 years of age.* The extremes given by different experimenters are, 35 ounces (Prout), and 81 ounces (Böcker). Almost every intervening number between these two remarkably different quantities has been stated by one observer or another to be the usual average. Great differences therefore exist, even in healthy adults; and the amount will vary with the quantity of fluid ingested, the external temperature and consequent activity of the cutaneous transpiration, the nature and quality of the food, the temperament of the body, and perhaps even with national peculiarities. Dr. Ed. Smith, from daily experiments made throughout the year, has shown that during a cold summer (half-year from May to October) the average quantity was somewhat more, whilst during a hot summer it was somewhat less than during the winter six months. With alcohol given to prisoners there was an average decrease of 20 ounces per day for three days, the quantity of water drunk being unchanged. With a day of rest the quantity was less than on days of labour, and there was more on treadwheel days, notwithstanding that the quantity of water drunk was the same, and there was more perspiration with the hard labour. Women secrete somewhat more urine than men,† and children nearly twice as much in proportion to the weight of the body. Some time, however, usually elapses after birth before the kidneys begin to discharge their function with activity, the urine up to the third day being usually scanty, albuminous, destitute of urea, and containing but a small proportion of solid ingredients. In infants from eight to eighty days of age the quantity of urine discharged varies from 250 to 410 cub. cent. ($\frac{1}{2}$ to $\frac{3}{4}$ of a pint) per diem, and is almost always acid.‡

364. The secretion of urine is considered to be essentially the product of two factors, one of which is the difference of pressure between the circulating blood and the excreted urine, whilst the other is the amount of urinary material which the blood contains.§ But it must also be connected with the activity of the cells lining the renal tubuli, whilst the influence of the nervous system and the composition of the blood probably form other factors. The influence of the blood-pressure is shown by the circumstance that when this is low the secretion is diminished; and if the pressure fall below 40 mm. Hg it is entirely arrested: on the contrary, when the blood-pressure is high, the secretion is augmented. The ordinary amount may be estimated at 120–140 mm. Hg, whilst the pressure of the urine in the ureters varies from 10–40 mm. Hg. That the quantity of the secretion is not exclusively dependent upon the blood-pressure is shown by the fact‖ that injection of a large quantity of distilled water into the veins of an animal promptly arrests the secretion. Moreover, if solution of sugar be injected into the veins, polyuria results without increase of blood-pressure; whilst the injection of a solution of gum augments the blood-pressure, but greatly checks or altogether arrests the secretion of urine. It may be observed that the pressure of the blood in the renal vessels is not always identical with that of the system generally, since, although it must necessarily fall when the aortic pressure falls, it may be reduced considerably below that in the systemic arteries generally, by any

* This number agrees very exactly with the careful experiments of Dr. Ed. Smith and Kaupp, "Archiv. f. Phys. Heilk.," Band xiv. † Donders, "Physiologie," p. 485.

‡ Pollack, "Jahrb. f. Kinderheilk.," N.F., Band ii. p. 27.

§ See Bernard, "Leçons," 1859, t. ii. p. 155. Ludwig and Goll, "Zeitschrift f. ration. Med.," Band iv. p. 93. Hermann, Virchow's "Archiv," Band xxxiv. Ustimowitsch, Ludwig's "Arbeiten," 1870, p. 198.

‖ R. Moutard-Martin and Ch. Richet, "Rev. Scient.," 1880, pp. 715 and 763.

cause leading to contraction of the renal arteries. In accordance with this, diminution or arrest of the secretion occurs both when the general blood-pressure has been diminished by bleeding, and also when the local tension has been reduced by compression of the renal arteries. In one of the experiments recorded by Goll, the urine being discharged by the ureters at the rate of 30 or 40 drops per minute, the animal was bled, when the flow immediately diminished to 12 drops per minute, but upon transfusing into its veins some blood taken from another animal it rapidly rose to 188 drops per minute. The same effect may be produced by acting on the renal circulation through the nervous system, as by irritating the pneumogastrics, which depresses the action of the heart, or by section of the spinal cord (Ustimowitsch), or of the sympathetic* at the lower part of the neck. Augmentation of the secretion, on the other hand, occurs when the pressure of the blood is either increased generally, as during digestion (Bernard), or locally in the renal capillaries, by ligature of the renal veins or of some of the larger systemic arteries, as the crural and axillary, or by the action of cold on the cutaneous capillaries. It may also be induced by division of the renal nerves, which, paralysing the vaso-motor system, allows the arteries to dilate and leads to a freer current of blood through the kidney. Vulpian found that section of the splanchnics is followed by similar, but less marked, augmentation, because such section also paralyses the vaso-motor system of the abdominal viscera generally, and, though allowing a fuller current of blood through the kidneys, lowers the blood-pressure as a whole.† Increased secretion of urine follows division of the pneumogastrics and puncture of the floor of the fourth ventricle. Hydruria is occasioned by mental emotions, fear being the one which most powerfully stimulates the kidneys to act, and the effect is observable both in animals and in man. It may act like cold by contracting the cutaneous arteries and producing congestion of the abdominal viscera generally, since diarrhœa is also frequently induced. The large flow of pale urine in Hysteria, as the attack is passing off, is well known; and occasionally this occurs as a critical discharge in some febrile affections. The importance of the other factor on which the secretion of urine depends is sufficiently demonstrated by the results of an experiment suggested by Ustimowitsch, who found that when the secretion of urine had been arrested by section of the spinal cord in the lower part of the neck, and common salt or urea was injected into the veins, secretion recommenced notwithstanding the great diminution of the blood-pressure consequent on the section, and with each additional gramme of sodium chloride injected, a very definite quantity (15–16 grammes) of water was discharged. So also when a large quantity of fluid has been absorbed within a short space of time, it is rapidly discharged by the kidneys, nearly all having escaped at the expiration of 2½ hours after the last portions have been taken.‡ The two kidneys do not secrete similar fluid at the same time, but one eliminates a more watery, the other a more saline fluid, alternately.—Curare administered in poisonous doses arrests or greatly diminishes the amount of urine secreted; Digitalis, probably, in part by augmenting arterial tension,§ and the inhalation of carbonic oxide gas increases it. It is a matter of common observation that injuries of the spinal cord are followed by changes in the constitution of the urine, which becomes ammoniacal and precipitates phosphates; but it appears

* Peyrani, "Comptes Rendus," t. lxx. p. 1300.

† Küss thinks that the serum of the blood naturally filters through the capillaries of the glomeruli, and that it is the function of the cells of the contorted portion of the tubules to reabsorb the albumin. ‡ Thudichum, "On the Pathology of the Urine," p. 26, 1858.

§ See Brunton and Power, "Centralblatt f. d. Med. Wiss." 1874, p. 497.

to be doubtful whether these changes are not the result of disordered secretion from the walls of the urinary bladder, the urine being secreted normally, but undergoing in its course through the urinary passages a kind of fermentation, which induces decomposition of the urea and the formation of carbonate of ammonia.*

365. The *Specific Gravity* comes to be a very important character in various morbid conditions of the urine; and it is therefore desirable to estimate it correctly. This also is, of course, subject to many causes of variation; since, when the same amount of solid matter is dissolved in a larger or smaller quantity of water, the specific gravity will be proportionably lower or higher; or, the quantity of water remaining the same, an increase or diminution in the amount of solid matter will raise or lower the specific gravity. It has been commonly supposed that the amount of solid matters in the urine bears such a constant ratio to its specific gravity, that the former may be approximately deduced from the latter; this, however, is now ascertained to be by no means the case.† Still, the determination of the specific gravity is of sufficient importance for diagnostic purposes to make it desirable to possess an average standard, as nearly approaching to accuracy as circumstances will permit. The average, according to Dr. Prout, in a healthy person, taking the whole year round, is about 1020; the standard rising in summer (on account of the greater discharge of fluid by perspiration) to 1025, and being lowered in winter to 1015. Simon, however, states the average specific gravity at no more than 1012. Dr. Roberts‡ observed the specific gravity of his own urine, while in a healthy state, to vary from 1001 to 1036. The first urine passed by infants has a specific gravity of 1010, and often contains columnar epithelium and remains of cells.§ In infants of a few weeks old the specific gravity varies from 1005–1007. That the specific gravity does not bear any constant relation to the quantity discharged has been shown by Dr. Hammond, who noticed that, although the afternoon and evening urine was most abundant, its specific gravity was very high, in consequence of its containing a large proportion of solid ingredients. The specific gravity of the urine probably depends mainly, in each individual case, upon the amount of azotized solids and of aqueous fluids habitually ingested, allowing for the portion of the latter that is dissipated by cutaneous exhalation; and it will also vary with the period that has elapsed since the last introduction of liquid into the stomach.

366. The amount of *solid matter* in 1000 parts of urine may vary from 20 to 70 parts; and hence the various recorded analyses of this liquid present very wide diversities in the proportion of its solid constituents.‖ The following

* Schiff (Lezioni, 1873, p. 329) has pointed out that injuries of the medulla oblongata cause hyperæmia of the kidneys, closely resembling the second stage of Bright's disease, which he attributes to paralysis of the vaso-motor nerves, whilst Brown-Séquard ("Comptes Rendus de la Société de Biologie," 1871, t. iii. p. 101, and "Lancet," 1871, vol. i. p. 6) attributes the congestion and hæmorrhages seen in the kidneys and other abdominal organs to contraction of the veins, or to simultaneous contraction of both arteries and veins. Ollivier (Archives de Médecine," Feb. 1874) gives various chemical observations showing the rapidity with which albumin appears in the urine after an attack of apoplexy.

† See Lehmann's "Physiological Chemistry" (Cavendish Society), vol. ii. p. 436.

‡ "Edinb. Med. Journ.," 1860.

§ Pollack, Loc. cit., and Martin and Ruge, "Centralblatt f. d. Med. Wiss.," 1875, p. 387.

‖ It is remarked by Lehmann (Op. cit., p. 447), that the urine of the French is poorest in solid constituents, especially in urea and uric acid, and that of the English the richest, that of the Germans being intermediate between the two; the ratio in each nation being in conformity with the proportion of animal food entering into its ordinary diet. These discrepancies, however, being chiefly due to the fluctuating amount of water, become very much

Table* will show the usual constituents of healthy urine, and the quantities excreted in 24 hours:—

Urinary Constituents.	Average quantity excreted in 24 hours, in grains.	Average quantity excreted for each 1 lb. avoird. of body-weight (estimating this at 150 lbs.), per diem, in grains.
Urea	512	3·5
Uric Acid	8·5	0·057
Allantoin	A trace.	—
Hippuric Acid	15	0·1
Kreatinin	15	0·1
Sugar		
Xanthin		
Acids: Paraphanic, Kryptophanic†, Phenylic, Taurylic, Damaluric, Damolic, Crystalline fatty acid, possibly Palmitic (Shunck), Oxaluric, Oxalic	Traces.	—
Pigment, especially Indican		
Mucus	7	—
Inorganic Salts (varying greatly in their relative proportions according to the nature of the food, and composed of)	140 to 380	0·933 to 2·53
Sulphuric Acid	17·34 to 41·14	0·115 to 0·27
Phosphoric Acid	31 to 79	0·207 to 0·526
Nitric Acid	A trace.	—
Silicic Acid	Traces.	—
Chlorine	51·87 to 173·2	0·345 to 1·154
Potassium	26·36 to 107·7	0·175 to 0·718
Sodium	79·75 to 171·0	0·531 to 1·14
Calcium	2·33 to 6·36	0·015 to 0·042
Ammonium	—	—
Ma4nesium	2·53 to 4·21	0·016 to 0·028
Iron‡	A trace.	—

less (as Simon pointed out) when we calculate the proportion which each principal component bears to 100 of solid residue; as is shown in the following Table:—

	Berzelius.	Lehmann.	Simon.	Marchand.
Urea	45·10	49·68	33·80	48·91
Uric acid	1·50	1·61	1·40	1·59
Extractive matter, Ammonia-salts, and Sodium Chloride	36·30	28·95	42·60	32·49
Alkaline Sulphates	10·30	11·58	8·14	10·18
Alkaline Phosphates	6·88	5·96	6·50	4·57
Phosphates of Lime and Magnesia	1·50	1·97	1·59	1·81

* Chiefly drawn up from the works of Parkes "On the Urine," 1860, Lond.; Thudichum, "On the Pathology of the Urine," 1858, Lond.; and Neubauer and Vogel, "On the Urine," Lond. 1863, New Sydenham Society's Translation; to which treatises the reader desirous of further information is referred.

† The presence of Paraphanic and Kryptophanic Acids is given on the authority of Dr. Thudichum ("Centralblatt," 1870, Nos. 13 and 14); his statements have been called in question by Pircher, "Centralblatt," 1871, p. 322, but he has reiterated them in Pflüger's "Archiv," Band xv. 1877, p. 466. He also admits the presence of Acetic and Formic Acids in the Urine, ibid. p. 15.

‡ See Thudichum, Op. cit.

It is difficult, if not impossible, to determine the exact mode in which the acids are distributed amongst the bases, but the Chlorides and Phosphates seem to be eliminated in the following proportions:—

	Grains in 24 hours.	
Sodium Chloride	about 250	
Ammonium Chloride	„ 35	
Magnesium Phosphate	„ 5	} Lehmann and
Calcic Phosphate	„ 10	} Kletzinsky.

The relation between the two last is reversed by Neubauer.

The urine contains, in addition, free carbonic acid, oxygen, and nitrogen gases; together with a certain and not inconsiderable quantity of extractive matters, consisting of substances whose nature has not been accurately determined, as in the case of those containing sulphur and phosphorus, the substance termed Oxide of Omichmyl by Scharling (which is apparently of a resinous nature), and others. The aggregate amount of the extractives is estimated by Dr. Parkes at 154 grains per diem, and constitutes an important field for future investigations. It will thus be seen that the total quantity of solid material eliminated by the kidneys does not fall far short of 900 grains in the 24 hours for a healthy adult man weighing 150 lbs., the proportion of organic compounds being about 550 grains, and of inorganic about 300 grains. The new-born child yields in 24 hours per pound of body weight less urea and chlorides, but it eliminates more phosphates and more water.*—Under the head of constituents not constantly, or not certainly, present, or perhaps present only in disease,† may be enumerated albumin, peptone, kreatin, xanthin, sarkin, grape-sugar, inosite, diastatic and proteolytic ferments,‡ glycin in combination with benzoic acid, forming hippuric acid,§ lactic and oxalic acids, fatty substances, blood and biliary colouring matters, salts of the biliary acids, allantoin, leucin, and tyrosin, succinic acid, cystin, inosite, taurin, hæmatin, pus, spermatozoa, carbonate of ammonia, phosphate of ammonia and magnesia, and sulphuretted hydrogen,‖ besides various substances consumed as food and eliminated by the kidneys, as the colouring and odorous matters of various vegetables and certain metals. The acid reaction of the urine depends essentially on the presence of the acid phosphate of soda; and the curious observation has recently been made that in dialysing the neutral phosphate of soda, the acid phosphate appears on the other side of the septum.

367. The most important of the organic constituents of the Urine is that which, from its being the principal source of the characteristic properties of the secretion, is termed *urea*.¶ Its chemical relations are stated to be best explained upon the hypothesis that it is the biamide of carbonic acid.** It contains 46·6 per cent. of its weight of Nitrogen. This substance exists preformed in the blood in the proportion of from 2 parts (in renal venous) to 4 parts (in renal arterial blood) in 10,000. It possesses the power of dialyzing through animal membranes with remarkable facility, almost equalling carbonate of potash in this

* Parrot and A. Robin, "Archives de Med.," 1876, p. 319.

† Abeles, "Centralblatt f. d. Med. Wiss," 1879, p. 387.

‡ Albertoni, "Centralblatt," 1878, p. 642; and Brunton and Power, "Centralblatt," 1878, § Especially in infants at the breast (Pollack, loc. cit.).

‖ v. Gorup-Besanez, "Phys. Chemie," p. 510.

¶ Urea, $CO(NH_2)_2$, contains 46·7 per cent. of nitrogen, and is isomeric with ammonium cyanate, $CNNH_4O = \left.\begin{matrix} C'' \\ H_2 \\ H_2 \end{matrix}\right\} N_2$, and with carbamide, $\left.\begin{matrix} O'' \\ H_2 \\ H_2 \end{matrix}\right\} N_2 + CO_2$.

** Miller's "Chemistry," vol. iii. p. 615.

respect.* It is eliminated by the cells of the renal tubuli.† The absolute quantity of urea eliminated in 24 hours, varies with age, season, weight of body, food, and occupation, and has been made a subject of examination by various chemists. The subjoined Table‡ gives the results of some of the more recent analyses; and from the examination of such tables we may draw the conclusions, that the average quantity of urea discharged by a man of good bodily health, on full animal diet, is about 500 grains per diem; and that children of from 3 to 7 years of age excrete, proportionately to their weight, about double the quantity of urea per diem excreted by men in adult life, the quantity still further diminishing in old age. The minimum amount excreted by an adult whilst fasting and at rest is about 2 grains per 1 lb. of body-weight. In infants at the breast Pollack (loc. cit.) found the quantity to vary from 15 to 30 grains per diem.

Season.—Dr. Ed. Smith,§ in the course of the year, found that the daily quantity (in himself) varied from 219 to upwards of 700 grains, the average upon the whole being 519 grains. The proportion to each 1 lb. of body-weight was, on the whole average, 2·76 grains. But in experiments in prison, either with or without hard labour, the proportion varied from 3·72 to 5·82 grains to each 1 lb. of body-weight; so that he is of opinion that the relative proportion is of no scientific value. There was increase with diminished temperature and with increased atmospheric pressure, and hence variations in the relations of these two agencies varied the results. The increase in the elimination of urea with cold was often deferred until the following day. The period of elimination is not that of production, and whatever increases elimination of urine increases that of urea also. G. Schleich‖ found that on exposure of the body to a water-bath, at a temperature of 100°—108° F. for about an hour, the daily amount of urea eliminated was always increased, the augmentation sometimes lasting to the third day.

Period of the Day.—The greatest hourly elimination of urea, in Dr. Smith's

* See Weikart, Wagner's "Archiv d. Heilkunde," 1862, p. 119.
† M. Nüssbaum, Pflüger's "Archiv," Band xvii. p. 591.
‡ Partly taken from Dr. Day's "Physiolog. Chemistry," 1860.

——	Age in years.	Weight in lbs. avoird.	Grains of Urea excreted in 24 hours.	Proportion of Urea excreted to 1000 parts of bodyweight in 24 hours.	Ditto for every 1 lb. of body weight.	Authority.
Man	38	153·7	459·2	0·42	3	
Boy	3	29·8	207·7	1·03	6·96	Rümmel.
Boy	4	31·7	240·2	1·08	7·57	
Girl	5	36·9	280·2	1·08	7·59	
Youth	18	129·1	562·1	0 62	4·36	
Man	31	163·7	604·9	0·5	3·69	
Man	65	127·9	295·2	0·33	2·31	
Boy	3	35	65·7	0·53	1·9	Bischoff.
Youth	16	107	305·8	0·41	2·85	
Girl	18	145	310·9	0·30	2·14	
Woman . . .	43	107	389·9	0·28	3·63	
Man	45	237	579·5	0·35	2·44	
Man	42	196	519	—	2·73	Ed. Smith.

According to Hofmann the healthy adult man eliminates in 24 hours from 22-43 grammes of urea = 0·37–0·6 per kilo of his body weight, the average being 34 grammes = 0·5 per kilo. The healthy adult woman from 16–28 grammes = 0·36—0·43 per kilo; on the average 25 grammes = 0·4 per kilo ("Zoochemie," 1879, p. 404).

§ "Proceedings of the Royal Society for May 30, 1861," and a private communication.
‖ "Archiv f. Exper. Pathol.," Band iv. p. 82.

experiments, occurred after the breakfast and tea meals; whilst it was least during the hours of the night and early morning. Ranke found that it steadily diminished from the morning to the evening.

Sex.—According to Dr. Parkes, the quantity of urea excreted every 24 hours, for 1 lb. of body-weight is, for men, about 3½ grains; for women, about 3 grains. During menstruation, according to Beigel, the excretion of urea diminishes, but subsequently it is increased.

Food.—Variations in the quantity and quality of the food occasion great differences in the proportion of the urea. The Table below* gives the results in grains of some of the best observers.

The immense amount of urea discharged upon a highly albuminous diet is worthy of particular notice. The quantity of urea always increases after food, attaining its maximum usually about the third or fourth hour, and this would correspond with the period when digestion and absorption being completed the interstitial changes in the cells and tissues throughout the body are being performed with the greatest activity. When an animal is fed on fat and water exclusively, or on starch and fat, with a very small admixture of albuminous compounds, or on sugar, the excretion of urea falls even below the proportion found in absolute starvation,† apparently because when no food, or an inadequate quantity of flesh-food, is given, the animal consumes some of its own flesh in order to maintain its temperature, and thus more Nitrogen is eliminated than when fat is supplied; for this, by combining with the Oxygen, keeps up the temperature, and spares the tissues of the animal. It is certain that nearly the whole of the Nitrogen consumed as food is eliminated by the urine in the form of urea. Thus, in an experiment made by Professor Parkes,‡ extending over sixteen days, two men who consumed in that period 313·76 grammes of Nitrogen in their food, discharged by the urine in the same time 303·66 and 307·257 grammes of urea respectively, the difference being made up by the fæces and other excretions. Every grain of urea may be regarded as proceeding from the disintegration of 3 grains of Protein, and represents the amount of work performed in raising 1·4 ton through one foot. So that on the supposition that 501·28 grains are eliminated in the day, the amount of work performed would amount to 218,786 kilogrammeters, or 704 foot tons (Haughton). Genth§ has shown that an increase in the quantity of water drank is followed by a marked increase in the quantity of urea eliminated, and this especially if the water be taken, not between, but at, meat times. Certain substances consumed with the food increase the quantity of urea excreted; amongst these are Urea itself and Uric Acid, common Salt (Voit), Phosphoric Acid (Böcker), Glycin, Guanin, Theobromine, Cubebs,

* ——	Ranke.*	Lehmann.†	Haughton.‡	Warnecke.§		Kölliker and Franque.‖
				Man.	Woman.	
I. Mixed Diet . . .	463–617	501·76	576	520	414	586·7
II. Highly Animal Diet	1332	821·37	—	—		1420
III. Vegetable Diet . .	264	347·10	394	389·6	310	447·7
IV. Non-azotized Diet .	264	237·90	—	—		262·48

† Ludwig, p. 381, vol. ii. ‡ "Proceedings of the Royal Society," 1867, No. 94.
§ "Untersuch. uber den Einflüss des Wassertrink. auf den Stoffwechsel," 1856.

* "Grundzüge der Physiologie," 1872, p. 509.
† Lehmann, "Phys. Chem." (Cav. Soc. ed.) vol. ii. pp. 450–452.
‡ Haughton, "Dublin Quart. Journ.," 1859. § "Dub. Med. Press," 1859.
‖ Vierordt, "Phys.," 1860.

and Cantharides.* On the other hand, it is diminished by Digitalis, Arsenic, Turpentine, and Alcohol.

Exertion.—The influence of muscular exertion on the excretion of Urea is a subject to which great attention has been directed during the last few years, as being likely to afford some insight into the source of muscular energy, and to show whether the force exerted by muscle is derived from the disintegration and oxidation of its own proper substance, or whether it proceeds from the oxidation of certain constituents, and especially of the hydrocarbonaceous constituents of the blood, the heat derived from which the muscular tissue is capable of converting into mechanical force. In the former case we should naturally expect that the nitrogenous products of the disintegrated muscular tissue would appear in the urine, in the latter we should anticipate an increase in the amount of carbonic acid and water eliminated from the body, without material increase in the excretion of Nitrogen by the urine. The facts of the case, as will be seen, are opposed to the view that the tissue of the muscle is materially disintegrated during exercise, and in favour of the view that the energy is derived from the oxidation of hydrocarbonaceous compounds. The experiments of Dr. Ed. Smith were amongst the first to show that muscular exercise was not attended with any notable increase in the amount of Urea eliminated. He found that with violent labour, as that of the treadwheel, there was only an increase of 19 grains daily over that of light labour. On Sunday there was an increase with increase of food; but in prisoners without variation of food, with spare systems, and with increase in the fæces, there was a decrease. Similar results were obtained by Voit,† who, in consequence of the very small differences that occurred in the quantities of urea eliminated in fasting animals (Dogs) with and without work, believed that such slight increase of urea as really occurs after severe labour, is due to increased thirst and ingestion of water, together with increased rapidity of the movements of the heart and lungs. Lehmann's‡ experiments also showed that no increase of urea took place in those engaged in active exercise. In 1866 an important experiment bearing on this point was made by MM. Fick and Wislicenus.§ These observers investigated the variations occurring in the amount of Nitrogen eliminated by the urine during the ascent of the Faulhorn, one of the peaks of the Swiss Alps, and about 6500 feet in height. They took no albuminous food for seventeen hours previously, nor during the ascent, which occupied eight hours, nor for six hours after, their diet consisting of biscuits of starch, fat, and sugar. The examination of the urine gave the following results:—

	The average quantity of Nitrogen excreted per hour was, by	
	Fick.	Wislicenus.
1. Urine of the night previous to the ascent—a period of 12 hours	0·63 gramme.	0·61 gramme.
2. Urine of the period of ascent—8 hours and 10 minutes . .	0·41 „	0·39 „
3. Urine excreted for 6 hours after the ascent	0.40 „	0·40 „
4. Urine of the night following the ascent, after a good meal had been taken—10½ hours	0·45 „	0·51 „

Here there was evidently a decrease in the excretion of nitrogen during and after exercise, but it must be remembered that no nitrogenous food was consumed. Very similar results were obtained by Professor Haughton,‖ who found that with about five miles of daily walk the amount of urea eliminated

* v. Gorup-Besanez, "Physiolog. Chem.," p. 540, 1862.
† Henle and Meissner, 1860, p. 373.
‡ "Archiv des Vereins für Wissenschaft. Heilkunde," vol. iv. p. 484, 1860.
§ "Lond. Phil. Mag.," 1866, p. 485. ‖ Lecture, "Brit. Med. Assoc.," 1868.

was 501·28 grains per diem, whilst when the exercise was increased to 20·74 miles of horizontal walk for five consecutive days, the amount of urea was 501·16 grains; actually less than the previous average. Two still more complete series of experiments have been conducted by Professor Parkes* on two soldiers, in the first series of which he investigated the elimination of nitrogen by the kidneys and intestines, during rest and exercise, on a diet without nitrogen; whilst in the second series the men were placed on a regulated diet of nitrogen. In the first series of experiments the men were kept for a first period of six days on ordinary diet and occupation, in order to determine the conditions present in perfect health, and to serve as a ground of comparison. Then for a second period of two days' duration the men were kept on a non-nitrogenous diet and remained at rest. Under these circumstances the urea fell from 35 grammes (which was about the usual daily amount with ordinary diet), to 16·7 in one man, and in the other from 26 to 15 grammes, or in both to about one-half its ordinary amount. During the third period of four days, the men returned to their usual diet and occupation, by which time they were considered to have regained their ordinary condition, and the quantity of urea excreted rose to its ordinary amount. During the fourth period of two days, the men were again placed on non-nitrogenous diet, but on this occasion were made to take severe exercise; walking on the first day 23·76 miles, and on the second day 32·78 miles. It was found that during the first thirty-six hours there was a decrease; but in the last twelve, or rest-hours of the forty-eight hours, an increase in the amount of urea; and that, on the whole, the effect of the exertion of walking fifty-six miles on a non-nitrogenous diet was a total increase of only 1·589 gramme of nitrogen in one man, and in the other of only 0·223 gramme in the forty-eight hours. In the fifth period the men once more returned to their ordinary diet and occupation for four days, in which a considerable increase of nitrogen over the average amount was observed; which however is referred by Dr. Parkes, not to the elimination of the products of destroyed muscle during the work-period, but to an excess of nitrogenous food consumed in the four days following the exercise. In the second series of experiments two men were kept on the same nitrogenized diet for sixteen days. For four days they were kept at their ordinary employment; during two days rested; returned to ordinary work for four days; took very active exercise for two days, walking twenty-four and thirty-five miles, and were then for four days more on ordinary occupation. The changes that took place in the urea were almost identical with those in the total nitrogen eliminated, and so nearly equal to that in amount, that (allowance being made for what passed by the bowels) it was certain none passed off, either during rest or exercise, by the skin or lungs. The results were, that in the first period the amount of urea was almost precisely the same in the two men. In the rest-period it increased nearly two grammes daily in each man, fell during the third period to the former average, decreased greatly during the first thirty-six hours of the exercise-period as compared with the rest-period, and increased in the last twelve hours; in the last or after-work period it also increased, though in a less proportion than the total nitrogen. The first series of these experiments undoubtedly corroborate the statement of Fick and Wislicenus, that on a non-nitrogenous diet exercise produces no notable increase in the nitrogen of the urine; although, when the subsequent period is also considered, it does produce a slight increase. The second series showed that, with an unchanged amount of nitrogen ingested, so far from there being any increase, there was an actual diminution in the amount of

* "Proceed. Roy. Soc.," Nos. 89, 94, 1867.

urea eliminated both during ordinary and during severe exercise, as compared with rest. There was, on the other hand, an excess, not great but long-continued, in nitrogenous excretion after exercise; and there was a retention of the nitrogen in the system when it was again supplied after both rest and exercise, and greatest in the latter case, showing that it is needed in the system, and that an insufficient supply at one time must be subsequently made up. In some recent experiments by Weigelin,* it appeared that if, after two hours of strenuous muscular exercise, the amount of urea eliminated during the succeeding two hours were determined, an increase of as much as 50 per cent. on the ordinary average was sometimes observed. Persistent muscular effort (tetanus) was found to produce more urea than the alternate contraction and elongation of muscle. In 1870 and 1871 a very important and complete series of observations on the effects of protracted and severe muscular exercise upon the excretion of nitrogen were made by Dr. Austin Flint, aided by several other physiologists.† The subject of the experiment was Mr. Weston, who in the first instance walked 100 miles in twenty-one hours and thirty-nine minutes, and subsequently attempted to walk 400 miles in five consecutive days; which, however, he failed to accomplish. Dr. Flint made a careful examination of the urine for five days preceding the walk, for the five days of the walk, and for five days after the walk. Mr. Weston was thirty-one years of age, and his weight was about 120 lbs. He smoked in moderation, and was an almost total abstainer from alcoholic fluids. On the first day of the walk he made 80 miles, on the second 48, on the third 92, on the fourth 50, and on the fifth 40. The failure occurred on the fourth day, from vertigo, partly induced by want of sleep. During the five days of the walk Mr. Weston consumed in all 1173·80 grains of nitrogen in his food, and eliminated 1807·60 grains of nitrogen in the urine and fæces. This leaves 633·80 grains of nitrogen over and above the nitrogen of the food, which must be attributed to the waste of the tissues, and probably almost exclusively to the waste of the muscular tissue. Lean meat, as has already been shown, contains about three per cent. of nitrogen (§ 337). The loss of 633·80 grains of nitrogen would then represent a loss of 21,127 grains, or 3·018 lbs. of muscular tissue. The actual loss of weight was 3·450 lbs., which allows 0·43 lb. loss unaccounted for, which might be fat or water. It would hence appear that there was a distinct consumption of muscular substance during the immense exertion of the period of five days' walking. In two days after the walk, the weight of the body had been made up to within four ounces of the normal weight. Schultzen and Nencki‡ have shown that Leucin and Glycocol administered to dogs greatly increase the amount of urea eliminated. Tyrosin causes no increase, but is expelled unaltered. Cerebral activity§ and sexual excitement‖ augment the quantity of urea.

Frequency of Micturition.—Kaupp¶ has shown that with increased frequency of micturition there is an increase in the quantity both of urine and of urea discharged in twenty-four hours.

Disease.—The amount of urea eliminated increases in the early stages

* Reichert's "Archiv," 1868, p. 207.

† See "New York Medical Journal," June, 1871, pp. 609–697. The subject has been again discussed by Dr. Pavy, "Lancet," 1876; and by Dr. Austin Flint in Humphry's "Journ. of Anat. and Phys.," 1878, vol. xii. p. 91. Dr. Flint endeavours to prove that the source of muscular power is to be sought in the destruction of muscular substance.

‡ "Zeits. für Biologie," 1872. § Byasson, "Rev. d. Cours Scient.," 1868, Thesis.

‖ Haughton, loc. cit., found the ordinary quantity of urea to be in the sheep 256 grains per diem, but in the ram during the rutting season 1493 grains per diem.

¶ "Archiv f. Phys. Heilk.," 1856.

of nearly all acute diseases,—meningitis, pneumonia, typhus, &c.,—indicating the rapid disintegration of the nitrogenous tissues and constituents of the blood, and coinciding with the period during which increased heat of skin is usually complained of. This, though not more than 4° or 5° Fahr. above the average, represents (from Newton's law of cooling) an increase of one-eighth of the total amount of heat produced—an amount equivalent to the force required to raise the body through one mile of vertical height per diem,* and furnishing an adequate explanation of the extreme exhaustion experienced by the sufferers at this period. Vogel and Warnecke found that in a case of typhoid fever no less that 1065½ grains of urea were excreted daily, or more than double the usual average, and in a case of pyæmia the extraordinary quantity of 1235½ grains. Now as every four grains of urea excreted correspond to five tons lifted through one foot, it is obvious that an enormous amount of force is spent in these diseases, fully accounting for the extraordinary debility induced in such patients. When the fever is over, the quantity of urea falls below the normal amount, in spite of the augmented quantity of nitrogenous food ingested, which is doubtless appropriated to the repair of the wasted tissues, and it then, after perfect recovery, returns to the normal standard. During convalescence it gradually subsides, and may even fall below the normal amount. The proportion appears to be remarkably diminished in some forms of hepatic disease. Thus Frerichs,† in a case of acute atrophy of the liver, found no trace of urea in the urine, but in its place leucin and tyrosin. In another case, recorded by Vogel, of cancer of the liver, scarcely one-fourth of the normal quantity of urea was found in the urine; and Heller has shown that the proportion of urea is diminished in chronic nervous affections, and in anæmia, however produced.‡

368. Next in importance to urea among the organic products of the metamorphosis of the azotized constituents of the tissues or of the blood, but ordinarily bearing a very small proportion to it (1 : 45 or 50) in quantity, is *Uric Acid* ($C_5H_4N_4O_3$). This compound contains 33 per cent. of nitrogen. It probably exists in the urine, partly in the free state, and partly combined or conjugated with the alkaline phosphates.§ The variations in the daily quantity eliminated are considerable; and, according to Ranke, whilst in great measure independent of differences in age, sex, height, weight, or temperature, stand in close relation with the ingestion of food, diminishing to a minimum of 3·7 grains with abstinence, and rising to a maximum of 32·5 grains on a full meat diet. Professor Haughton found the average quantity elimininated by those consuming animal food to be 4·55 grains per diem, whilst vegetarians discharged only 1·48 grains. Pollack‖ found that the quantity was relatively large in infants at the breast, varying from 1·5 to 3 grains per diem. It is diminished after the use of alcohol (Hammond), and after the administration of quinine (Ranke), and is totally absent when large draughts of water have been taken (Genth). It is increased after the free use of tobacco (Hammond), and after the consumption of certain substances introduced into the food, as glycin and urea, but no influence is exerted on its quantity by mental activity or repose (Byasson). The effects of muscular exercise were found by Austin Flint¶ to cause slight increase, the quantity passed by Mr. Weston in his long walk of 317½ miles in five days, being at the rate of three grains per diem, whilst during the five days previous to the walk it was 2·26 grains, but the quantity varied considerably on each day, without it being possible

* Haughton, Op. cit.
‡ Gmelin, vol. viii. p. 325.
‖ Loc. cit.
† "Deutsche Klinik," 1855, p. 31.
§ Byasson, "Rev. d. Cours Scient.," 1867–8, p. 610.
¶ "New York Med. Journal," 1871, p. 687.

to connect this variation with the composition of the food or the amount of the exercise taken. A marked increase has been observed in intermittent fevers, in leucæmia, in peritonitis, phlebitis, and some chronic renal and spinal affections. Uric acid is found in the spleen-pulp in considerable quantities, and also in the lungs, liver, pancreas, and brain; in the juice of muscles, and in small quantities in the blood (Garrod) in the form of an acid urate of soda or ammonia.* It seems, therefore, to be very generally present where active interstitial changes are taking place. The *precipitation* of uric acid (usually in combination with potash, soda, and ammonia, and perhaps sometimes with lime), which frequently takes place on the cooling of the urine, must not be regarded as indicative of the presence of an unusual amount of this substance; since it may depend upon other conditions. It seems to have been clearly proved by Dr. Bence Jones,† that there is no relation whatever between the *acidity* of the urine, and the *absolute amount* of uric acid which it may contain; for in the urine which is most acid, and which deposits the largest uric-acid sediment, very little uric acid may really exist; whilst that which contains most uric acid may hold it in perfect solution, and may have but a feeble acid reaction. The main cause of the deposit of uric acid sediments, is doubtless the presence of some other acid; for the addition of any acid to healthy urine passed soon after food, is always sufficient to produce it. But the deposit takes place less readily if the temperature of the fluid be high, since the solvent power of the acid phosphate of soda is then more strongly exerted; so, on the other hand, a deposit often takes place in urine which would not otherwise exhibit it, through an unusual reduction in its temperature, as by exposure to the cold air of a sleeping-room in the winter. Again, the deposit of uric-acid sediment is favoured by concentration of the liquid, which thus augments the proportion of the urate to the water, and at the same time intensifies the acid reaction; and thus urine whose constituents are otherwise normal, may throw down a copious deposit of this kind, merely from deficiency of water; whilst an unusual amount of uric acid may be really present without being deposited—the urine, too, exhibiting its ordinary acidity—if the proportion of water be large. Thus the uric-acid sediment may be regarded as dependent upon three concurrent conditions:—(1) Decrease of temperature; (2) Increased proportion of uric-acid compound to the water, positively or relatively; (3) Increased acidity of the urine. Sometimes one condition is most influential, sometimes another; but they are all usually concerned in some degree.—There are many diseases, especially those of a febrile nature, in which the presence of an *excess* of uric acid is a very marked symptom; there is often, at the same time, a reduction in the proportion of urea; and thus it would seem that, with perhaps an augmented tendency to disintegration of the tissues, there is an incapacity for the performance of that higher process of oxidation, which is requisite for the genesis of urea; so that a larger proportion of the products of the 'waste' passes off in the state of uric acid, as in animals whose respiration is feeble.

The proportion of *Hippuric Acid* ($C_9H_9NO_3$) present in the urine appears to be in great measure dependent upon the nature of the food and upon the amount of exercise. According to the researches of Weissmann and Thudichum, it amounts to between 30 and 40 grains per diem on a mixed diet. On a purely animal diet, it falls to about 12 grains per diem; whilst it rises considerably when vegetables alone are consumed; and its origin has been

* Thudichum, "Pathology of the Urine," p. 97.

† See his 'Contributions to the Chemistry of the Urine,' in "Philos. Trans.," 1849.

attributed by Sheppard and Meissner* to the conversion at the kidney of a substance existing in the cuticle of plants nearly allied to Kinic acid. As might be anticipated, therefore, a large quantity of this acid is constantly present in the urine of Herbivora, but only traces exist in that of Carnivora. Both Mack and Roussin found that horses at rest pass much urea and little Hippuric acid: but when at work, the quantity of Hippuric acid equalled or exceeded that of urea, the absolute quantity of the latter undergoing a diminution equal to the increase of the Hippuric acid. As urea is one of the ultimate products of oxidation in the body, whilst Hippuric acid is very imperfectly oxidised, it would seem that during violent exertion the due oxidation of the secondary nitrogenous compounds produced by the disintegration of the tissues is interfered with, perhaps by the diversion of the oxygen to form carbonic acid, the quantity of which has been shown by Dr. Ed. Smith to be so notably increased by all kinds of muscular exertion; or we may, with more probability, suppose that the lungs are unable to eliminate the whole of the carbon of the disintegrated tissues in the form of CO_2, and that a part of the carbon is consequently discharged by the kidneys in the form of the richly-carbonized compounds, Hippuric or Benzoic acids. The quantity of Hippuric acid eliminated can be greatly increased by the administration of benzoic, succinic, cinnamic, or kinic acids, or of oil of bitter almonds.† The transformation of benzoic into Hippuric acid appears to take place at the liver, as it does not occur in jaundiced patients, or in dogs in whom the ductus communis choledochus has been tied, the Benzoic acid then passing off unchanged. The process is exceedingly simple. Benzoic acid ($C_7H_6O_2$) + Glycin (C_2H_5NO) or Glycocol ($C_2H_5NO_2$) producing Hippuric acid ($C_9H_9NO_3$) + $2H_2O$. Kühne and Hallwachs, however, maintain that the conversion occurs in the blood, and Meissner and Sheppard at the kidney.—*Kreatin* ($C_4H_9N_3O_2 + H_2O$) and *Kreatinin* ($C_4H_7N_3O$) may be obtained by the action of Chloride of Zinc on concentrated urine; but the researches of Heintz‡ have shown that no Kreatin is present in fresh urine, that which was formerly obtained being in fact produced by the decomposition of the Chloride of Zinc compound, the Kreatinin of which takes up water and is converted into Kreatin.§ The quantity of Kreatinin daily eliminated by a healthy man, living on a good mixed diet, was found by Neubauer to vary from 9 to 20 grains. The maximum quantity is excreted on a flesh, the minimum on a farinaceous diet (Meissner, Voit). In dogs, exertion causes no increase. Kreatinin is the most powerful organic base in the body. Kreatin which is chiefly derived from the nervous system can be converted by boiling with Baryta water into Sarcosin and urea.‖—When ingested with the food it is either eliminated unchanged, or it is partially converted into Kreatinin.¶ The colouring matters of the urine appear to be derivatives of the biliary acids, and not of the biliary colouring matters, since Bogomoloff** and Heynsius and Campbell†† found that injection of the biliary acids into the blood increased the quantity of urinary colouring matter, whilst injection of biliary pigments was without effect. Masius, and Vanlair‡‡ thought they proceeded from the colouring matter of the bile which underwent conversion in the intestines into stercobilin, and was partially excreted in the fæces and

* "Centralblatt," Nos. 43 and 44, 1866.

† See Matschersky, Virchow's "Archiv," 1863, p. 528.

‡ Vogel and Neubauer, "On the Urine," New Syd. Soc. Transl., 1863, p. 18.

§ Kreatinin $C_4H_7N_3O + 4H_2O$ becoming Kreatin $C_4H_9N_3O_2$.

‖ Kreatin $C_4H_9N_3O_2$ becoming Urea $C_2H_4N_2O$ and Sarcosin $C_3H_7NO_3$.

¶ Meissner, "Centralblatt," 1868, p. 275.

** Bogomoloff, "Centralblatt f. d. Med. Wiss.," 1875, p. 201.

†† Pflüger's "Archiv," Band iv. p. 497. ‡‡ "Centralblatt f. d. Med. Wiss.," 1871, p. 369.

partially eliminated by the kidneys. Jaffe* considered stercobilin to be identical with urobilin, since the absorption striæ of its solutions is the same, and it gives the same beautiful green fluorescence with chloride of zinc. Maly† obtained from the intestines a substance to which he has applied the term Hydrobilirubin, which he considers to be a derivative of cholepyrrhin, and to undergo partial absorption.‡ They may all be regarded as modifications of one substance, *urobilin*, which gives a yellow or rose colour dichroising into pink with mineral acids, and presents an absorption stria between *b* and F.§ These bodies, as was also noticed by Carter,‖ present close analogies to the series of compounds of which indican forms the first member, and a blue colouring matter is sometimes generated in disease. The researches of Schunck and Carter long ago showed that indican was a constituent of healthy urine, and Prof. Senator (1877) found that it is contained in remarkable quantity in the urine of those who take little food and who vomit, or fail to digest what they consume. The greater the degree of anæmia, the more pronounced is the excretion of Indican. It is particularly abundant in those suffering from carcinoma of the stomach.¶ The extractives of the urine contain considerable proportions of carbon, whilst they are poor in nitrogen; so that their increase will be favoured by an excess of carbonaceous food, an imperfect action of the liver, and a low degree of respiration; whilst, on the other hand, a highly-azotized diet, especially if combined with active exercise, will tend to their reduction.—The odour of the urine appears to be due to the presence of minute quantities of the volatile acids, termed by Städeler, Phenylic (or Carbolic, C_6H_5OOH), Taurylic ($C_{14}H_8O_2$), Damaluric ($C_{14}H_{11}O_3H_2O$, and Damolic, the composition of which last is unknown. Béchamp has described a ferment under the name of "Nephrozymose" which can be obtained from urine by precipitating it with three times its volume of alcohol of 90 per cent. It is an albuminous body, and is capable of converting starch into sugar at a temp. of 60°–70° C.

369. The determination of the mode and place of origin of the urinary constituents, and especially of the urea and uric acid, are points of considerable interest. The solution of this question, however, demands great skill in chemical analysis, and the evidence is at present in an extremely unsatisfactory state. As regards the *mode* of origin of urea, its composition shows clearly that it proceeds from the disintegration of the albuminous or nitrogenous constituents of the tissues and blood. It was at one time considered that it was generated entirely at the expense of the muscular tissue; but as no one has yet succeeded in extracting urea from muscle, and as muscular exertion, even when violent and protracted, causes little or no increase in the amount eliminated, and as the substances that we know result from the disintegration of muscular tissue, as kreatin and kreatinin, and either not at all, or not easily, converted into urea, and even when ingested are eliminated, unchanged, without causing any augmentation in the amount of urea, whilst a large increase quickly follows the ingestion of nitrogenous food when the body is at rest, there seem to be good grounds for admitting that only a portion of the urea discharged can proceed from that disintegration to which the muscles, in common with

* "Centralblatt f. d. Med. Wiss.," 1871, p. 465. † Idem., 1871, p. 851.

‡ See also Schunck, "Proceed. of Roy. Society," 1867, vol. xvi. p. 73.

§ Thudichum, "Chemical Physiology," 1872, p. 187, gives directions for obtaining Urochrom, Uromelanin, Uropittin, Omicholein, Omicholic acid, and Xanthin, which last, Scherer and Neubauer also considered to be present in the urine.

‖ "Memoirs of Manchester Med. Soc.," vol. xiv. p. 293. See also Kletzinsky, Heller's "Archiv," vol. vi. p. 414; and Thudichum, "Brit. Med. Journ.," Nov. 5, 1864.

¶ "Medical Examiner," August 7, 1877.

all other animal structures of high organization, are liable, and that another, and much larger portion is derived from the decomposition and disintegration of the albuminous compounds that are constantly being consumed in maintaining the activity of the great glandular and cellular organs of the body,* the ultimate results of the oxidation—urea, carbonic acid, and water—being the same. Numerous experimenters† have recently endeavoured to solve the question by examination of the urine in reference to the amount of urea eliminated after the administration of acids; of alkalies, especially of salts of ammonia, and of substances standing in more or less intimate chemical relationship with urea, such as the amido-acids and asparagin; and the most important outcome of these experiments seems to be that the production of urea and uric acid are not altogether the result of analytical processes, but that they proceed in part from synthetical processes. Hellerworden, for example, concluded from his experiments that the formation of ammonia precedes that of urea, and that a part of the ammonia is applied to the neutralisation of acids, whilst the excess is converted into urea. Schmiedeberg fed dogs with ethylamin carbonate, and obtained crystals of ethyl-urea; and he has hence been led to maintain that all compounds which contain the group NH_2—CH_2—are decomposed in the body with separation of ammonia, which then passes into the condition of carbonate, and finally by synthesis into urea.

The question of the *place* of origin of the urea is still more difficult to answer. Up to a very recent period it was universally held that the kidneys constituted a kind of filter by which certain products of the disintegration of the tissues were separated from the blood and discharged from the body. M. Picard's experiments, which showed that urea is uniformly present in the blood (2-4 parts in 10,000), and in larger proportion in the renal arterial than in venous blood, and those of Gréhant,‡ showing that after ligature of the ureters the amount of urea in renal venous blood becomes exactly equal to that in renal arterial blood, have been commonly referred to in support of this view, the small quantity present being attributed to the care with which the system was freed from this excretory product. Lately, however, an attempt has been made to prove that urea is formed from the secondary products of the disintegration of the tissues, such as kreatin, kreatinin, uric acid, hypoxanthin, and taurin, in and by the kidney itself, upon the following grounds.§—First, that extirpation of the kidneys is followed by only a trifling increase in the proportion of urea present in the blood, though the proportion of kreatin and other lower stages of the oxidation of nitrogenous compounds is augmented both in the blood and muscles; secondly, that after ligature of the ureters, the renal

* On this view the "luxus consumption" of Voit and others, which was considered to consist in the oxidation of the nitrogenous constituents of the food in the blood previous to their conversion into tissue, has no existence.

† O. Schultzen and Nencki, "Zeitschrift f. Biologie," Band viii. p. 124; Knieriem, ibid., Band x. p. 263; xiii. p. 36; Feder, ibid., Band xiv. p. 161; Weiske, Schrodt, and St. v. Dangel, ibid., Band xv. p. 261; Munk, "Zeitschrift f. Physiolog. Chemie," Band ii. 1878, p. 29; Salkowski, ibid., Band i. p. 374; iv. p. 54; Schröder, ibid., Band ii. p. 228; Gähtgens, ibid., Band iv. p. 36; Schmiedeberg, "Archiv f. Experim. Pathol.," Band viii. 1878, p. 9; Hellerworden, ibid., Band x. p. 125; Picard, "Comptes Rendus," t. lxxxvii., p. 993.

‡ See abstract of Memoir in Humphry and Turner's "Journal of Anat. and Phys.," 1871, p. 216.

§ See Munk, "Deutsche Klinik," 1862, p. 299; Oppler, Virchow's "Archiv," 1861, Band xxi. p. 260; Subotin, Henle and Meissner's "Zeitschrift," Band xxviii. 1866, p. 114; and Zalesky, "Untersuchungen über den Uræmischen Process." Schultzen and Nencki ("Zeits. f. Biologie," 1872, Band vii. p. 124) believe that some of the intermediate stages between Albumin and Urea are represented by Glycol, Leucin, and Tyrosin. But Küssner has clearly shown that Tyrosin cannot be regarded as an antecedent of Urea ("Centralblatt," 1875, p. 216).

organs remaining intact, there is considerable increase in the amount of urea contained in the blood; thirdly, that the ingestion of kreatin with the food produces an increase of the excretion of kreatinin and urea; fourthly, that on rubbing down kreatin with the substance of the kidney, it is rapidly converted into urea; and lastly, that there is reason for believing that the cells covering the glomeruli, exercise a secreting function, and are not merely adapted for the elimination of water, since these glomeruli are abundantly distributed through the kidneys of birds, the urine of which animals is semi-solid, whilst it is impossible to obtain a trace of uric acid from their blood. Now, in opposition to some of these statements are the observations of G. Meissner,* who, by analysing large quantities of blood, obtained unmistakable evidence of the presence of uric acid in that of the bird (goose), and shows by calculation that it is possible for all the uric acid excreted by the animal to have been separated from the blood passing through the kidney in a given time. In the course of his experiments, Meissner found so much uric acid in the liver, and so little in other organs, that he came to the conclusion that the liver was the seat of its formation in birds.† On extending his researches to mammals, he found that here also the liver presented on chemical analysis a larger proportion of the essential urinary constituent urea than any other organ. Hence he concludes that it proceeds from the disintegration of the hæmoglobin of effete blood-corpuscles into urea, glycogen, and biliary colouring matter; and adduces pathological evidence, derived from the observations of Frerichs, Städeler, and Harley, to the effect that in acute and chronic atrophy of the liver it is either greatly diminished or wholly absent. Heynsius further adduced in support of this view the fact that more urea can be obtained from a liver which has been removed from the body for some hours and kept at a temperature of 104° F. than from a fresh one, and Cyon‡ maintained that the blood which was passed through the liver of a living animal is richer in urea after its passage than before. These statements have, however, been again called in question by Gscheidlen in an elaborate essay§ upon the subject, and his experiments have led him to the conclusion that no single organ can be fixed upon as exclusively producing urea, but that it is formed in the system generally. It is remarkable that though it can be detected in the blood, liver, spleen, kidneys, brain, and eye, it does not appear to be present in the muscles. Gréhant‖ finds that after extirpation of the kidneys, the amount of urea in the blood undergoes progressive increase, proportionate in fact to the quantity that would have been excreted had the kidneys been in action; he finds also that after ligature of both ureters the same accumulation of urea takes place, and that the renal venous blood, contrary to Picard's statement, contains less urea than renal arterial blood, whilst after ligature of both ureters the proportion of urea in the arterial and renal venous blood is equal. There seems therefore to be good reason for believing that urea is simply excreted by, and not formed in, the kidneys.¶ In reference to the origin of urea from kreatin, Meissner states, in opposition to Munk,** that he has found no increase in the

* "Centralblatt," 1868, pp. 226 and 275.

† Pawlinoff ("Centralblatt," 1873, p. 241) has satisfied himself that uric acid is not formed in, but only excreted by, the kidneys.

‡ "Centralblatt," 1870, p. 580. For a good resumé of all this discussion, see Parkes' Lectures, in the "Lancet," 1871, vol. i. p. 467.

§ See abstract of his memoir in "Centralblatt," 1871, p. 630.

‖ "Centralblatt," 1870, p. 249.

¶ See the corroborative experiments of Rosenstein, "Centralblatt," 1871, p. 353; Falck, Virchow's "Archiv," Band liii., 1871, p. 282; Gscheidlen, "Studien über den Ursprung des Harnstoffs im Thierkörper," Leipzig, 1871.

** "Deutsche Klinik," 1862, p. 299.

amount of urea when kreatin or kreatinin were given with the food, or otherwise introduced into the blood. In all instances these substances were discharged either unaltered, or merely with conversion of some of the kreatin into kreatinin. Voit* also declares himself opposed to the view that the formation of urea occurs at the kidneys, except in so far as that it may take place to some slight extent from a conversion of kreatin; though when this was given with food it was eliminated partly unchanged and partly converted into kreatinin. He found an increase in the quantity of urea in the blood, and also discovered it in the muscles, both after extirpation of the kidneys and after ligature of the ureters: the amount being larger in proportion to the lateness of the period at which death occurred, and on that account it was smaller in amount after ablation of the kidneys. In one instance, after extirpation had been performed, he collected the whole of the retained urea, and obtained 5·3 grammes, whilst, if the animal had been allowed to live, he would have eliminated 5·8 grammes in the same space of time. No increase of kreatin occurred either after extirpation or ligature. Respiration of oxygen diminishes the quantity of urea in the urine,† though it augments the activity of the combustive processes, and might therefore be expected to increase it. An explanation of this may be that it leads to the combustion of the urea itself and its conversion into carbonic acid, ammonia, and water, The non-increase of urea in the urine when violent exertion is made is, perhaps, explicable on the same view. On the whole, the results of recent researches seem to show that urea is formed in the tissues generally, including the renal, and with the exception perhaps of the muscular, and that thus entering the blood from many quarters, it is filtered off by the kidneys, the secreting cells of which have a special affinity for it.

370. Besides its organic materials, the urine contains a considerable amount of *Saline* matter; the excretion of which, in a state of solution, appears to be one of the principal offices of the kidney. The total quantity of fixed salts eliminated per diem by men on mixed diet varies from 140 grains to 378 grains, and by women from 158 to 303 grains. Various saline compounds are being continually introduced with the food; and others are formed within the system, by the oxidation of the sulphur and phosphorus of the tissues or of the food, and by the combination of the sulphuric and phosphoric acids thus formed, with alkaline and earthy bases which the food may contain, usually in a state of combination with weaker acids which are otherwise disposed-of. Thus the saline compounds found in the urine are to be regarded as partly proceeding from the retrograde metamorphosis of the materials of the tissues after these have served their purpose in the economy, and partly from that of such components of the food as, being superfluous, do not undergo organization. But the kidney also serves as the channel for the elimination of saline compounds introduced into the system *per se;* these being sometimes normally present in the body, but ingested in too large an amount, as is often the case with common salt; whilst, on the other hand, they may be altogether foreign to the composition alike of its solids and its fluids.—The *Alkaline Sulphates* usually constitute, as we have seen (§ 366), at least 10 per cent. of the whole solid matter of the urine. Being always in solution, however, they never make their presence known by the formation of sediments, and are only to be detected by chemical tests. The causes which influence their amount have been carefully studied by Dr. Bence Jones, who has shown that they vary (like urea) with the amount of food ingested, and with the degree of nervo-muscular activity put-forth; as might be anticipated from the fact, that, under

* "Centralblatt," 1868, p. 468. † Ritter, "Revue Scientif.," 1872, p. 91.

ordinary circumstances, the sulphuric acid is entirely formed within the system, by the oxidation of the sulphur of the protein-compounds, the bases being furnished by the alkaline carbonates or phosphates of the blood. A portion of the sulphur is, however, eliminated by the bowels in the form of taurin. In Mr. Weston's case the average excretion of sulphuric acid for five days before his long walk of 317½ miles in five days was 38·37 grains, for the five days of the walk 53.50 grains, and for the five days after the walk 49·02 grains. In regard to the effects of exercise on the excretion of acids by the urine, Klüpfel* found that it was augmented to the extent of 44·8 per cent. by exercise, whilst Sawicki† obtained only variable and chiefly negative results. When sulphuric acid or soluble sulphates are taken into the system *per se*, they partly find their way out of it by the kidneys; the proportion of sulphuric acid in the urine being for a time augmented, although the increase is not considerable until some hours have elapsed after the introduction of these substances into the stomach.‡ They are not increased on a non-nitrogenous diet by exercise (Parkes). The absolute amount of sulphuric acid varies from 35 to 50 grains per diem. Normal human urine contains more *phosphoric acid* than is required for the salination of the lime and magnesia bases in the urine. The normal amount eliminated per diem is from 30 to 40 grains. It is more abundant after animal than after vegetable food. The acid is ordinarily generated within the system, by the oxidation of the phosphorus originally introduced in the protein-compounds; and thus, as in the case of the sulphates, the quantity of its salts which is excreted by the urine bears a certain relation to the amount of these compounds ingested as food, and also to the amount of muscular tissue which has undergone disintegration by exercise. But it further appears that there is a special relation between the quantity of the alkaline phosphates in the urine, and the amount of disintegration of the *nervous* tissue; as might have been suspected from the fact, that this tissue is distinguished by the very large proportion of phosphorus, united with fatty acids, which it contains. And a marked increase of these salts is observed in those inflammatory diseases of the brain, in which there is reason to believe that an unusually-rapid disintegration of its texture is taking place.§—The *Earthy Phosphates* usually bear but a small proportion to the alkaline; but their presence in the urine comes to be of great importance with reference to the precipitates which they form in particular conditions of that secretion. From the researches of Dr. Bence Jones (loc. cit.) it appears, that the quantity of these phosphates in the urine chiefly varies with the amount of them contained in the food, into many articles of which they enter largely,‖ but he has also ascertained that their formation within the system is determined by the presence of their bases; for if any earthy salt, a little chloride of calcium or sulphate of magnesia, for

* Hoppe-Seyler's "Chem. Unters.," 1868, Heft 3. † Pflüger's "Archiv," Band v. p. 285.
‡ Dr. Bence Jones in "Philosophical Transactions," 1849.

§ See Dr. Bence Jones' valuable series of Papers in the "Philosophical Transactions" for 1845, 1847, and 1850, and in the "Medico-Chirurgical Transactions" for 1847 and 1850: also Byasson, Op. cit., p. 612. It is curious to observe, that whilst the increase in the alkaline phosphates in Inflammatory affections of the nervous centres is very marked, there appears to be a positive diminution of them in Delirium Tremens. A certain allowance must be made, however, for the abstinence from food, which will of itself occasion a reduction in the quantity excreted.

‖ The experiments of Neubauer ("Journal f. pract. Chem.," 1866, p. 96), Riesel (Hoppe-Seyler, "Med. Chem. Untersuch.," Heft 3, 1869), and Soborow ("Centralblatt, f. d. Med. Wiss.," 1872, p. 609) all show that when taken in excess the salts of lime are very rapidly and completely eliminated by the urine, the whole being discharged in the course of a few hours.

instance, be taken into the system, the quantity of earthy phosphates in the urine undergoes an increase. The small quantity of carbonate of lime taken into the system with the food, or set-free by the slow disintegration of the osseous tissue, is probably excreted in Man almost entirely in the form of phosphate; although of the much larger amount ingested by herbivorous animals, a considerable proportion is excreted in the urine in its original state. The Earthy Phosphates, although insoluble in water, are soluble in all acid liquids; and they are held in solution in Urine, like the urates, by the acid phosphate of soda. Their precipitation in an alkaline state of the urine is owing to the want of this solvent, not to an excess in their production; for as Dr Bence Jones has pointed out, that excess of alkaline and earthy phosphates in the urine which constitutes the true 'phosphatic diathesis,' is generally coincident with a highly-acid state of the urine. In Mr. Weston's case before alluded to the average secretion of the phosphoric acid was 50·14 grains per diem for the five days before the walk, for the five days of the walk 76·63 grains, and for the five days after the walk, 56·89 grains. The excretion of phosphoric acid is not increased by exercise on a non-nitrogenous diet (Parkes). The absolute amount excreted per diem on a mixed diet varies from 54 to 78 grains (Genth).—The only other inorganic saline constituent of the Urine, whose quantity gives it importance, is *Chloride of Sodium*. By far the larger proportion of this is doubtless derived directly from the food; but little being furnished by the disintegration of muscle, which will set free potash rather than soda. The amount eliminated by the urine is consequently subject to great variation, the function of the Kidneys being to remove whatever is superfluous, and thus to prevent the blood being overcharged with this substance. The average quantity is 250 grains, but in Ranke's experiments on his own person, the quantity discharged varied from 75 to 523 grains daily. Of the chloride of sodium introduced as food, a part appears to undergo decomposition in the system, whereby hydrochloric acid is furnished to the gastric fluid, and soda to the bile; much of this acid, however, must reunite with its base in the alimentary canal, so that the chloride of sodium thus regenerated will be absorbed with the products of the digestive operation. Its quantity is increased by muscular exertion (Byasson). Dr. Flint found the average amount daily excreted during five days in the person of Mr. Weston to be 159·45 grains for 5 days previous to a walk of 317½ miles. During the walk the average was 65·08 grains, and during the five days after the walk 312·40 grains per diem. The quantity is decreased on a non-nitrogenous diet (Parkes.) It is much diminished after profuse sweating (Ranke), and in many diseases, especially in inflammation of the lungs. In febrile affections the potassium salts are eliminated in larger proportion than those of sodium. In convalescence the opposite prevails.* The amount of *Ammonia* excreted by the urine varies from 0·83 to 0·61 grammes (12·8—9·4 grains) per diem.† The administration of the mineral acids augments the quantity considerably,‡ the increased production of ammonia having the advantage of preventing the acids introduced into the system from combining with and carrying off the fixed alkalies, the presence of which is so indispensable for life,§ and lending some support to the view of Schmiedeberg,‖ that in the decomposition of the tissues ammonia is first formed and then urea.—

* Salkowski in Virchow's "Archiv," Band liii. p. 209.
† Neubauer, Fehling's "Handwörterb. der Chemie," Band iii. p. 559.
‡ Walter, "Archiv f. Exp. Pathol. u. Pharmacol.," Band vii. 1877, p. 148.
§ C. Gaehtgen's "Zeits. f. Phys. Chemie," Band iv. 1880, p. 36.
‖ "Archiv f. Exper. Pathol. und Pharmacol.," Band viii. 1878, p. 9.

Although *Nitric Acid* can scarcely be regarded as a normal constituent of the Urine, yet the investigations of Dr. Bence Jones* appear to show that it is formed by a combustive process within the body, whenever ammoniacal salts are introduced into the system; its amount, however, being very small. He has also found that it is generated after the ingestion of small quantities of urea; a fact which affords some confirmation to the doctrine of Frerichs, that urea may undergo decomposition into carbonate of ammonia, whilst still circulating in the current of blood.—The presence of *Oxalic Acid* in the urine (in combination with Lime) has been usually regarded as a pathological phenomenon, consequent upon an irregular performance of the retrograde metamorphosis of the tissues; but there can be no doubt that it may also result from the presence of soluble salts of oxalic acid in certain articles of vegetable food.†—The Gases found in the urine have been examined by Planer‡ and Bernard.§ Planer found in one instance 7, and in another 16 per cent. of gas. The following Table gives the percentage composition of the gases obtained:—

In 100 parts of Urine at 32° F. and 30 in. Bar.		Percentage Composition of the Gases amongst themselves.		
		Planer.		Bernard.
Nitrogen	0·820	15·2	7·2	18·64
Oxygen	0·043	0·5	0.5	2·55
Carbonic Acid free	4·729	84·3	92·3	78·81
„ „ combined	3·066			
		100	100	100

About one-third of the carbonic acid was combined, the remaining two-thirds were free.

371. The ordinary *acid* reaction of the Urine appears to be due, not to the presence of any free acid, but to the conversion of the *basic* phosphate of soda into the *acid* phosphate by the subtraction of a part of the base, which occurs when uric, hippuric, lactic, or other free acids come into contact with the former substance. There is no adequate reason to believe, that, in the healthy state, there is ever any other cause than this; although in morbid urine free organic acids are almost certainly present.‖ The urine becomes more acid after elimination, the reason of which is not known. It has been shown¶ that the acid reaction is far from being constant in degree, even when an ordinary mixed diet is steadily employed; for that it varies at different periods of the day, increasing and decreasing *inversely with the acidity of the stomach.* Thus the acidity of the Urine decreases soon after taking food, whilst that of the Stomach is increasing, and attains its lowest limit about three to five hours after a meal, when, therefore, absorption is being most actively performed. An alkaline reaction is often observed in the

* "Philosophical Transactions," 1851.—It is right to state, however, that this doctrine has been called in question by some eminent authorities, who deny the validity of the test for nitric acid employed by Dr. Bence Jones.

† See Dr. Golding Bird on "Urinary Deposits."

‡ v. Gorup Besanez, "Physiolog. Chem.," 1862, p. 526. § "Leçons," vol. i. 1859, p. 347.

‖ See Prof. Lehmann's "Physiological Chemistry" (Cavendish Society's ed.), vol. ii. pp. 404–406.

¶ Dr. Bence Jones, "Philos. Transact.," 1849; with whose observations those of Roberts, "Memoirs of Manchester Phil. Society," 1859; and Brunton, "Digitalis," p. 62 agree.

urine at this period, which, according to Dr. Roberts, is due to the presence of fixed alkali; this occasions a precipitation of earthy phosphates, rendering the urine turbid, though the quantity of uric acid at this period is always large. The acidity then gradually increases, whilst that of the stomach is decreasing; and attains its highest limit after a fast of some hours, when the stomach is quite empty, and its secretion neutral. If no food be taken, the acidity does not decrease, but remains at nearly the same point for ten or twelve hours. When *animal* food was alone employed, the diminution of the acidity after a meal was more marked and continued longer than when a mixed diet was eaten (apparently on account of the greater demand for acid in the stomach); and the acidity did not rise quite so high after fasting as with a mixed diet. On the other hand, when the diet was purely *vegetable*, the diminution of the acidity of the urine was never such as to render it absolutely alkaline, although its acidity was reduced to the point of neutrality; and the increase of its acidity after fasting was sometimes very considerable, though by no means so marked as the decrease of alkalescence.—These diurnal variations in the acidity of the urine make it highly probable that corresponding variations occur in the alkalescence of the blood; such diurnal variations being produced by the quantity of acid separated from it, and poured into the stomach for the purpose of dissolving the food. The introduction of dilute sulphuric acid into the stomach, even in large doses, was not found to produce any decided change in the acidity of the urine; the only perceptible effect being a slight diminution of the decrease which takes place after taking food, and a slight augmentation of the increase after fasting. On the other hand, the use of liquor potassæ in large doses lessens the acidity of the urine, preventing it from rising after fasting to the height it would otherwise attain, and increasing its alkalescence after a meal; but it does not render the urine by any means constantly alkaline, nor does it hinder the variations produced by the state of the stomach from being very evident. Tartaric acid in large doses temporarily increases the acidity of the urine, causing it to rise considerably higher than usual after a fast, but not preventing that which is passsed a few hours after food from becoming alkaline. Tartrate of potash in large doses, on the other hand, has a marked effect in rendering the urine alkalescent; still it does not prevent the usual recurrence of the acidity some hours after a meal.—The Urine of Herbivorous animals, except during inanition,* is *alkaline;* partly because their food contains a large quantity of alkaline and earthy bases, in combination with citric, tartaric, oxalic, and other acids, which are decomposed within the system; and partly because the amount of sulphuric and phosphoric acids, generated as products of the oxidation of the elements of the tissues or of the surplus-food, is not sufficient to neutralize them. Such is the condition which occasions the alkalinity of Human Urine, when a portion of the acid which would otherwise show a predominance is directed into another channel; and it is exaggerated in those states, in which, either from the irritating nature of the food, or from the irritable condition of the stomach, an undue quantity of acid is poured out into that viscus; so that, its reaction being habitually acid, that of the urine becomes habitually alkaline. Such a state of the urine must be carefully distinguished, as Dr. Bence Jones has pointed out,† from that in which the alkalescence is due to the presence of *volatile*, and not to that of *fixed* alkali; the difference being easily recognizable by the influence of the liquid upon reddened litmus-paper, for the restoration of

* The hippuric acid naturally present is then replaced by uric acid.

† "Medical Times," Dec. 13, 1851.

its blue colour is permanent in the latter case, but only transitory in the former. The alkalescence due to the presence of volatile alkali is due to the decomposition of urea, whilst the urine is yet within the bladder, through the agency of morbid secretions of that viscus; and it disappears when this organ returns to its healthy state. On the other hand, the alkalescence from fixed alkali proceeds from disordered action of the stomach, which is usually connected with disorder of the general system; and it persists until this can be remedied. In both forms of alkalescence there is a precipitation of earthy phosphates; but in the alkalescence from fixed alkali the precipitate usually consists almost entirely of phosphate of lime: whilst in that from volatile alkali, the amorphous sediment of phosphate of lime is mingled with prismatic crystals of the phosphate of ammonia and magnesia. These precipitates may be obtained from healthy urine, by adding to it a solution of potash or of ammonia; and the decomposition of such urine, which begins to take place very soon after it leaves the body, gives rise to the same precipitation, by the production of carbonate of ammonia, at the expense of its urea.

372. Thus, then, we have seen that the Kidneys serve as the special instruments for depurating the Blood of those *highly-azotized* compounds, which are formed in the system by the decomposition of the materials of the albuminous and gelatinous tissues, and also by that of the non-assimilated components of the food. We have seen, also, that they serve for the removal of certain excrementitious compounds, of which *carbon* is a principal ingredient; and these, although normally present in but small amount, may undergo a marked increase in disease, especially when the liver is insufficiently performing its functions, or the respiratory process is obstructed. Further, we have been led to regard the Kidneys as the emunctory, not only for the superfluous water of the blood, but also for those saline compounds, which, having been introduced into the system or generated within it, in larger amount than is compatible with the normal constitution of the blood, or than is required for the reparation of the solids of the body, or for the production of its fluid secretions, are only fitted for elimination. On this point a very elaborate series of researches was made by Wöhler,* who showed that of the soluble salts taken into the circulation, those are most readily excreted which produce a determination of blood towards the kidneys, whereby an increased quantity of liquid is filtered-off through the outlet which they afford. This statement is to be extended from saline compounds, to such other soluble matters as are not eliminated by preference through other channels, or are present in too large an amount to find their way out thence with sufficient rapidity, as Sugar and Lactic acid. In like manner, too, the system makes an effort to free itself (so to speak) from various substances altogether foreign to it, which have been introduced into the circulating current by absorption, and which would be injurious if retained; the rate at which it does so being in a great degree dependent upon the functional activity of the Kidneys.

373. It is a most important fact, in a Dietetic and Therapeutic point of view, that the metamorphic process, of which the greater part of the constituents of the urine are the products, should be capable of retardation or of acceleration by the presence of other substances in the blood. The former appears to be the operation of *thein*, which is the active principle of Tea and Coffee. From various experiments,† it appears that the use of these substances, by retarding the "waste" of the system, diminishes the demand for

* Müller's "Elements of Physiology," translated by Baly, p. 589.

† Böcker, "Archiv des Vereins für gem. Arbeit. zur Förd. der Wiss. Heilk.," 1854; and Julius Lehmann, "Annal. der Chem. und Pharm.," Band lxxxviii.

food, and makes a limited amount of it go further;* and this conclusion seems fully borne out by experience.†—The like results happen, according to Dr. Böcker, under the use of small quantities of Alcohol frequently repeated; as much as 13⅓ grammes less urea being excreted daily, when a teaspoonful of proof spirit was taken seven or eight times a day, than when water alone was drunk. It does not hence follow, however, that Alcohol can be used as advantageously for this purpose as Tea or Coffee; in fact, it may be doubted whether it is so much by diminishing the "waste" of matter, as by interfering with the due elimination of its products, that Alcohol occasions a diminution in the weight of the urinary solids. For, although it does not appear to effect any marked diminution, but rather an increase in the elimination of certain forms of excrementitious matter which have been received back into the blood, and especially of the hydrocarbonaceous products (§ 287, vi.), yet very cogent evidence is supplied by the experience of Zymotic diseases, that the very same cause produces an accumulation of fermentible azotized substances in the blood.—It seems not unlikely that the almost instinctive craving for Tobacco among a large proportion of mankind arises out of its possession of a power of retarding the metamorphosis of the tissues; since we find that men, when supplied with this article, can far better sustain being put upon a short allowance of food than when destitute of it.

374. Of the substances that accelerate the metamorphosis of the tissues, and thus augment the solids of the urine, the Alkalies and their carbonates and Chloride of Sodium are those whose action is best known; these (with such of their salts as are formed by acids which are decomposed in the blood into the carbonic, such as the acetates, tartrates, and citrates) have a solvent action on the albuminous compounds generally, and tend to break-up these compounds into simpler forms of combination. Hence it seems likely that their presence in the Blood in increased amount will tend to hasten the retrograde metamorphosis of the tissues; their chemical force being exerted, not merely upon those which are already in a state of disintegration, but also upon those which, being disposed to degenerate, cannot exercise that resisting power which they possess when in a state of complete vital activity.‡ The operation of Liquor Potassæ in health, in acute rheumatism, and in chronic diseases, has been carefully studied by Dr. Parkes,§ and he has given satisfactory evidence that it causes an increase in the solids of the urine generally, but especially in the urea and in the amount of the sulphuric and phosphoric acids; thus clearly showing that it hastens the metamorphosis of some of the albuminous structures of the body. Similar results were obtained by Dr. Golding Bird,‖ from the employment of acetate of potash.—It does not appear, however, that the excretion of the urinary solids is augmented by those "diuretic" medicines which cause a large amount of liquid to be passed-off through the Kidneys, merely by determining an increased flow of blood to them. On the contrary, it would seem as if, by producing congestion and irritation, they sometimes interfere with the normal process of secretion;

* Dr. Ed. Smith ("Proceed. of Roy. Soc.," 1861) found the decrease in the elimination of urea after the use of tea (which had the greatest effect) and coffee to be but slightly marked after the first day or two.

† Voit, from experiments with coffee on a *dog*, was led to a different result; and considers that this substance possesses but little influence on the excretion of urea. See Henle and Meissner, "Bericht," 1860, p. 397.

‡ See Voit, "On the Action of Common Salt," &c., Munich, 1860.

§ "Brit. and For. Med.-Chir. Review," vols. xi. xiii. xiv.

‖ See his 'Lectures on the Influence of Researches in Organic Chemistry on Therapeutics,' in "Medical Gazette," 1848, vol. xlii. p. 230.

so that the quantity of solid constituents is actually decreased, notwithstanding the large augmentation in the watery part of the urine.* This very important fact has been demonstrated by Prof. Krahmer,† who gives the following as the result of his observations upon the amounts excreted in 24 hours, after the administration of diuretics to persons in health :—

Medicine given.	*Total Solids in Urine.*	*Organic Compounds.*	*Inorganic Compounds.*
None	2·40 oz.	1·28 oz.	1·13 oz.
Juniper	2·12 „	0·94 „	1·18 „
Venice Turpentine	1·94 „	1·11 „	0·83 „
Squill	2·25 „	1·04 „	1·21 „
Digitalis	2·45 „	1·28 „	1·17 „
Guaiacum	2·43 „	1·38 „	1·05 „
Colchicum	2·32 „	1·36 „	0·96 „

It seems highly probable that the 'critical evacuations' of urine, as of sweat or fæcal matter, on which the older physicians were accustomed to lay great stress, are really charged with noxious substances, of which the blood is thus depurated; and that great benefit would frequently arise in practice from the use of the 'alterative diuretics,' as suggested by Dr. G. Bird, where (as in chronic rheumatism, gout, &c.) there is reason to believe that a quantity of mal-assimilated matter exists in the system, of which it is important to get rid. In many such cases, indeed, clinical observation had already established the benefit derivable from such medicines, without affording the rationale of it.

375. The urine as it is secreted trickles drop by drop into the bladder, a musculo-membranous receptacle capable of holding from one to three pints, from which it is discharged at stated periods. The bladder is composed of two muscles opposed in action, the detrusor urinæ, which forms the greater part of the membranous bag, and the sphincter vesicæ, which forms its neck. Both are chiefly composed of unstriated muscular tissue, though some fasciculi of striated muscle are found in the sphincter, and both are under the governance of nervous centres situated in the lumbar portion of the spinal cord, though they may also be influenced by the emotions and the will. Under ordinary circumstances the escape of the urine is prevented by the moderate contraction or tone of the sphincter vesicæ, to overcome which in the rabbit the pressure of a column of water of from 16-20 inches in height,‡ and in the dog of about 30 inches is required. On section of the lower part of the spinal cord, or of the vesical nerves, the pressure of a column of water of only five or six inches in height is sufficient to force a passage for the fluid through the sphincter. The concordant observations of Masius§ and Budge‖ show that the motor centre of the bladder is situated at or about the level of the 4th lumbar Vertebra in animals. In connection with the motor centre there appears to be a second or inhibitory centre also situated in the lumbar region, for Goltz has shown¶ and observations on man furnish corroborative evidence that neither incontinence nor retention of urine need necessarily follow division of the spinal cord; but that in some instances the subjects of this injury can hold their water for several hours, and discharge it at regular intervals—that is to say, that whilst the bladder is filling, some influence restraining the action of the detrusor is exerted, which

* In the case of Digitalis Dr. Brunton found there was a considerable absolute, though not relative, increase in the amount of urea eliminated. See Brunton on "Digitalis," p. 42, 1868.

† Heller's "Archiv," Dec. 1847. ‡ Kupressow, Pflüger's "Archiv," 1872, Band v. p. 291.

§ "Bulletin de l'Acad. Roy. de Belgique," 1868, p. 491.

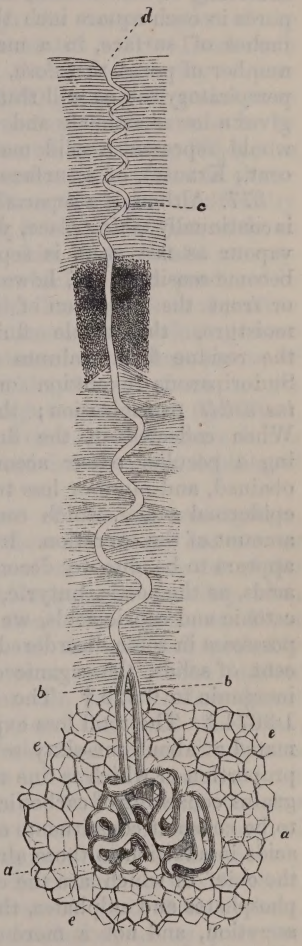
‖ Virchow's "Archiv," 1858, Band xv. p. 115. ¶ Pflüger's "Archiv," 1873, p. 474.

from analogy there is reason to believe proceeds from an inhibitory centre, till the excitation of the accumulated urine becomes so strong as to stimulate the motor centre and overpower the inhibitory centre. Goltz observed, and the experiment might be useful in cases of lesion of the spinal cord in man, that the application of a cold wet sponge to the anus caused immediate expulsion of the urine, either by stimulating the motor centre and inducing contraction of the detrusor, or by paralysing the inhibitory centre, and thus effecting the relaxation of the sphincter, and removing any obstacle to the respondence of the detrusor to the stimulus of the moderate accumulation of urine in the bladder. Daily experience teaches us that the will can exert an influence both on the motor and inhibitory centres situated in the lumbar region of the cord.

4. *Of the Skin;—Cutaneous Transpiration.*

376. The Skin is the seat of various secretions, as the Sebaceous, Ceruminous, and Odoriferous,—for each of which it is provided with special organs; but these have reference chiefly to its own protection, or to some other *local* purpose; and the only one which can be regarded as truly *excrementitious*, is the Transpiration of aqueous fluid holding certain matters in solution. The elimination of this fluid from the blood is effected by the *Sudoriparous* glandulæ (Fig. 180), which essentially consist of long convoluted tubes (*a*, *a*), rarely single, but usually multiplied by repeated dichotomous subdivision (*b*), sometimes also giving off short cæcal processes before their termination. These are seated beneath the Corium and in the midst of the subcutaneous adipose tissue rather than in the substance of the skin itself, and the glomerulus is always invested by a sheath of smooth muscular tissue (Krause).* The tubuli of each gland are lined with one or more layers of polyhedric epithelial cells, and unite so as to form but one duct; and this passes upwards through the Cutis and Cuticle, in a somewhat cork-screw like manner (*c*), to open upon the surface of the latter (*d*), which it usually reaches obliquely, so that the outer layer of the Epidermis forms a sort of little valve, which is lifted by the secreted fluid as it issues forth. These glandulæ are diffused in varying proportions over the entire surface of the body. According to Mr. Erasmus Wilson,† as many as 3528 of them exist in a square inch of surface on the palm of the hand; and since every tube,

Fig. 180.



Sudoriparous Gland from the palm of the hand, magnified 40 diam.:—*a*, *a*, contorted tubes, composing the gland, and uniting in two excretory ducts, *b*, *b*, which unite into one spiral canal that perforates the epidermis at *c*, and opens on its surface at *d*; the gland is imbedded in fat-vesicles, which are seen at *e*, *e*.

* Krause, "Centralblatt f. d. Med. Wiss.," 1873, p. 817.

† "On the Management of the Skin," 3rd edit., p. 37.

when straightened-out, is about a quarter of an inch in length, it follows that, in a square inch of skin from the palm of the hand, there exists a length of tube equal to 882 inches, or 73½ feet. The number of glandulæ in other parts of the Skin is sometimes greater, but is generally less than this; and, according to Mr. Wilson, about 2800 may be taken as the average number of pores in each square inch throughout the body. Now the number of square inches of surface, in a man of ordinary stature, is about 2500; the total number of pores, therefore, may be about *seven millions*; and the length of the perspiratory tubing will thus be 1,570,000 inches, or nearly 28 miles. Landois gives a lower estimate and estimates the number at about 2½ millions, which would represent a solid mass about equal to one-third of a kidney (77 cub. cent., Krause), or a surface of about 40 square inches.

377. Although a separation of fluid by this extensive glandular apparatus is continually taking place, yet this fluid, being usually carried off in the form of vapour as fast as it is separated, does not ordinarily accumulate so as to become sensible. If, however, from the increased amount of the secretion, or from the condition of the surrounding air as regards temperature and moisture, the whole fluid thus poured out should not evaporate, the residue forms minute drops upon the surface of the skin. Thus the Sudoriparous excretion may take the form either of *sensible* or of *insensible* transpiration; the latter being constant, the former occasional. When collected in the fluid state, sweat is a colourless liquid, possessing a peculiar odour according to the part of the skin from which it is obained, and more or less turbid from the presence of sebaceous matter and epidermal scales, which constitute from 0·2 to 0·3 per cent. of the whole amount of the excretion. Its reaction is alkaline.* The acidity often observed appears to be due to decomposition, and to the presence of certain volatile acids, as the acetic, butyric, and formic; to which, and possibly to the metacetonic and capric acids, we are probably to attribute the sour smell which it possesses in some disordered states of the system. It contains about 1·29 per cent. of solids, the organic constituents amounting to 0·962 per cent. and the inorganic to 0·329.† The index of refraction of sweat from the axilla is 1·3674.‡ The total loss experienced by an adult through the skin is estimated at about one-sixty-seventh of the weight of the body, by far the larger proportion of which is due to the elimination of water, only from 50 to 150 grains consisting of carbonic acid gas. The substances which have been found to be constant constituents of the sweat are, water, fat, various volatile fatty acids in addition to those already mentioned, urea and inorganic salts, amongst the chief of which are the chlorides of sodium and potassium, the alkaline phosphates and sulphates, the earthy phosphates, and iron. That it is a true secretion, and not a mere transudate, is shown by the entire absence of albumin, except under very unusual conditions, and then only occasionally.§ Other constituents of the sweat, whose presence is not constant, or the nature of which has not been satisfactorily determined, are the salts of ammonia, of lactic acid, and of the hydrotic acid of Favre, and certain pigmentary sub-

* Gillibert d'Hércourt, "Gaz. Méd. de Lyon," 1853, Trümpy, Pflüger's "Archiv," xviii. p. 494.

† The proportion of solid matter contained in different specimens differs very greatly; thus, according to Anselmino, it varies between 0·5 and 1·25 parts in 100; the observations of Favre ("Archives Génér. de Méd.," 1853, 5me Sér., tom. ii. pp. 1–12) give ·443 parts per 100 as the proportion contained in nearly nine gallons which he had collected; whilst those of Schottin ("Archiv für Physiol. Heilkunde," Band ii. pp. 73–104) raise it as high as 2·24 parts per 100, of which, however, 1·2 parts consisted of epithelium and insoluble matters.

‡ Valentin, Pflüger's "Archiv," 1879, Band xix. p. 84.

§ See Leube, Virchow's "Archiv," Band xlviii. pp. 181, 301; and "Archiv f. Klin. Med.," Band vii. p. 1.

stances of various shades. In disease, uric acid, grape-sugar, albumin, and biliary colouring matters have been found; and when taken with the food, benzoic acid (partly converted into hippuric), succinic, cinnamic, and tartaric acids, arsenious and arsenic acids, with iodine and iodide of potassium, have been recovered in the sweat. Funke calculates that about 11 grains of nitrogen are daily eliminated by the skin through the desquamation of the epithelial scales. He also found urea (as was first stated by Dr. Landerer*) to be a constant constituent. In one experiment, the entire quantity of perspiration for the whole body, for 1 hour, being 3320 grains, $6\frac{1}{2}$ grains were found to be present. If the secretion had continued at the same rate for 24 hours, $157\frac{1}{2}$ grains of urea would have been eliminated, containing $73\frac{1}{2}$ grains of nitrogen. Under ordinary circumstances, however, it is probable that a very much smaller quantity is thus eliminated. From the general uniformity in the proportion of solids in the fluid eliminated, it is obvious that, with an increase in the quantity of fluid excreted by the skin, there is also an augmented excretion of solids; and to the deficiency which is thus produced in the salts of the blood may be partly assigned the debilitating effects of profuse perspirations. Other causes, however, probably concur in producing those effects. Thus the great fatigue which is experienced as a consequence of muscular exertion in a heated atmosphere may fairly be set down to the diminished activity of the respiratory process at high temperatures (§ 287, 1), and the colliquative sweating of hectic fever is obviously not a cause but a consequence of, though it may also react upon and increase the debilitated state of the general system.

The secretion of sweat is under the influence of the nervous system, and the researches of Luchsinger† and others show that there are one or more sweat centres situated in the anterior horns of the grey matter of the spinal cord, and extending into the medulla oblongata, or possibly even lying in the cerebral convolutions. From these centres nerve fibres arise, which, in the case of the *posterior limbs* of the cat, and probably in other animals and man, emerge with the anterior roots of the lumbar nerves, especially with the second and third, but also with the last dorsal roots, and enter the cord of the great sympathetic, and then join the sciatic nerve, being ultimately distributed to the skin of the foot. Some fibres also emerge from the last lumbar and the sacral nerves and join the sciatic without first passing into the sympathetic system (Vulpian). The fibres for the *fore limbs* chiefly emerge with the anterior roots of third, fourth, and fifth cervical nerves, and join the first thoracic ganglion of the sympathetic, or pass directly into the branches of the brachial plexus to be distributed to the forefoot. The sweat centres may be excited by mental influences, as by fear, by heat, by venous blood, as in Asphyxia, by reflex stimulation, as by irritation applied to the leg of the opposite side or to other sensory nerves, and by various toxic agencies, as by Jaborandi or its active principle Pilocarpin, by Eserin, Picrotoxin, Nicotin, and Ammonium, Acetum, and by Muscarin. They are inhibited by cold and by Atropin. Stimulation of the centres or of the nerves causes a great and sudden increase in the amount of secretion produced, but no such effects are observed if the nerves be divided below the

* Heller's "Archiv," Band iv. p. 196. See also Deininger, "Deutsch. Archiv f. Klin. Med.," 1870, Band vii. 587.

† Luchsinger and Kendall, Pflüger's "Archiv," Band xiii. p. 212; Luchsinger, ibid., Band xiv. p. 545; Band xv. p. 482; Band xvi. p. 538; Ostroumow, Pflüger's "Archiv," Band xii. p. 219; Nawrocki, "Centralblatt f. d. Med. Wiss.," 1879, p. 257; Marmé, "Nachrichten d. Götting. Gesell. du Wiss.," 1878, No. 3; Ott and Woodfield, Foster's "Journal of Physiology," vol. i. p. 193; Adamkiewicz, "Die Secretion des Schweisses," Pamphlet, 1878; Vulpian and Raymond, "Comptes Rend.," t. lxxxix. p. 11; Strauss, ibid. p. 53.

point stimulated. On the other hand, on stimulation of the distal cut extremity the secretion immediately recommences, even when the temperature is low, and without any increase in the capillary circulation, showing that the secretion is not the result of simple transudation consequent on congestion of the vessels, but to the action of special gland cells. So entirely independent is it of the vascular system that it can be induced by appropriate stimulation even in a limb that has been severed from the body. If the abdominal sympathetic cord be cut in an animal on one side, and the creature be exposed to heat, no sweating occurs, but if the distal surface of the divided trunk be stimulated, sweat is exuded on the foot of the same side; but, if now the sciatic be divided, stimulation of the sympathetic fails to produce any further secretion. In man the secretion is always bilateral and symmetrical.

378. The entire loss by the Skin in 24 hours is 1-67th of the total weight. The amount of fluid which is "insensibly" lost from the Cutaneous and Pulmonary surfaces was estimated by Seguin at 18 grains per minute; of which 11 grains pass off by the skin, and 7 by the lungs. Funke,* with two students, made numerous experiments upon the amount and characters of the Sweats excreted from the hand and forearm under different circumstances. In these experiments the arm was enclosed in a caoutchouc bag, and each experiment lasted for one or two hours. It was found that the largest quantity of sweat obtained from the forearm and hand under favourable circumstances, in 1 hour, was 740 grains, which would, in 24 hours, supposing the secretion to continue at the same rate, amount to about $2\frac{1}{2}$ lbs. But, from accurate measurements, Funke ascertained that the ratio of the superficies of the forearm and hand to that of the body generally was 1 : 17; so that if the perspiration took place continuously and at the same rate from the whole surface of the body, upwards of 42 lbs. might be discharged in 24 hours. On the other hand, the minimum quantity excreted by the hand and forearm was 48 grains per hour, which would amount to 1152 grains in 24 hours, and this, multiplied by 17, would give $2\frac{3}{4}$ lbs. for the amount eliminated from the whole body in 24 hours. It was found, however, that different regions of the body gave off, in proportion to their surface, very different quantities of fluid: thus, in no instance was the amount discharged by the leg equal to that given off by the arm. Moreover, the three experimenters furnished very different proportions of sweat under the same circumstances: thus, with active exercise in the sun, the proportion between them was as 1 : 2·3 : 4·4, and in another experiment as 1 : 1·7 : 2·06. Funke draws the conclusion from his experiments, that the entire amount of perspiration from the whole body may fluctuate from about 2 ounces (819 grains) to about 29 ounces (12,588 grains) per hour, the quantity of solid residue varying from 14·25 to 107·57 grains per hour. Favre, by taking large quantities of warm drinks, and exposing the body to a high temperature, collected no less than 2560 grammes, or about $5\frac{1}{2}$ lbs. of water in $1\frac{1}{2}$ hours. It is difficult to give an average for the 24 hours when the variations are so great; but it may, perhaps, be estimated at about 2 lbs., the exhalation of aqueous vapour by the lungs being rather less than 1 lb. (§ 294). An interesting series of observations has been published by Dr. Victor Weyrich† upon the relative amounts of insensible perspiration under different conditions. The

* "Beiträge z. Kennt. der Schweiss;" Moleschott's "Untersuch." Band iv. p. 36.

† "Die unmerkliche Wasserverdünstung der Menschlichen Haut," Leipzig, 1862. See abstract in "Med.-Chir. Rev.," 1863, vol. ii. p. 359. See also Röhrig, "Die Physiologie der Hautathmung," "Deutsch Klinik," 1872, No. 23; and Erismann, 'Zur Physiologie der Wasserverdünstung von der Haut,' in "Zeitschrift f. Biologie," Band xi. pp. 1–78, 1875.

instrument he employed was a modification of Daniell's hygrometer; and his experiments extended over more than a year. He found that variations of temperature between 55° and 70° F., when the body was clothed, produced little effect; but every 1° C. (= $1\frac{4}{5}$° F.) above 70° F. occasioned an increase of 2 per cent. in the total amount of vapour exhaled, and for every 1° C. below 55° F. there was a diminution of from 1 to $1\frac{1}{2}$ per cent. He observed that the effects of the relative moisture of the air were in great measure concealed by variations in temperature, so that the highest averages of insensible perspiration occurred, not with the lowest, but with moderate amounts of moisture in the air. The minimum amount of perspiration always occurred on rising in the morning, being then 25 per cent. below the average. The maximum amount was eliminated at noon, when it rose to 52 per cent. above the minimum. Food invariably increased the cutaneous transpiration, coffee and tea having a particularly powerful influence. The increase occurred soonest after breakfast, but was greatest and most permanent after dinner. Moderate muscular or mental exertion slightly increased the amount of perspiration, but fatigue and exhaustion produced a considerable decrease. Violent muscular effort raised it to 77 per cent. above the mean; severe intellectual labour, 42 per cent. During sweating, the rise was equal to 116 per cent. over the mean, but after sweating it fell even to 26 per cent. below the mean. The amount of insensible perspiration varies greatly, with the conditions of the atmosphere, and of the body itself, in respect to exposure, food, exercise, and activity of other secretions; and these variations, as we shall hereafter see (§ 381), have a most important share in the regulation of the temperature of the body. According to Garrod* sweating begins when standing at rest at about 86° Fahr. Exact observations on this point, however, in which not merely the temperature, but the hygrometric state of the air should be precisely determined, are much wanting; the best hitherto recorded being those made by Dr. Southwood Smith† at the Phœnix Gas Works, in which the former element only was carefully noted. These observations were made upon eight of the workmen employed in 'drawing' and 'charging' the retorts and in making up the fires, during which they are exposed to intense heat; the men were accurately weighed in their clothes, immediately before they began, and after they had finished their work; and in the interval between the first and second weighings, they were not allowed to partake of any solid or liquid *ingesta*, nor to part with urine or fæces.

Experiment I. Nov. 18, 1836. Day bright and clear. Temperature of the air in which the men worked, 60° Fahr. Barometer 29·25 in. to 29·4 in. Duration of labour, 45 minutes.—Average loss of weight, 3 lbs. 6 oz.; maximum, 4 lbs. 3 oz.; minimum, 2 lbs. 8 oz.

Experiment II. Nov. 25, 1836. Day foggy, with scarcely any wind. Temperature of the air 39° Fahr. Barometer 29·8. Duration of labour, 75 minutes. Average loss of weight, 2 lbs. 2 oz.; maximum, 2 lbs. 15 oz.; minimum, 14 oz.

Experiment III. June 3, 1837. Day exceedingly bright and clear, with little wind. Temperature of the air, 60°. Duration of labour, 60 minutes.—Average loss of weight, 2 lbs. 8 oz.; maximum, 3 lbs.; minimum, 2 lbs.

Experiment IV. On the same day two other men worked in an unusually hot place for 70 minutes; the loss of weight of one of these was 4 lbs. 14 oz.; and of the other 5 lbs. 2 oz.

* "Journ. of Anat. and Phys.," vol. vi. 1872, p. 130.

† "Philosophy of Health," vol. ii. pp. 391–396.

Although the individuals subjected to those experiments were not in all instances the same, yet there was enough of identity among them to admit of the certain inference, that the amount of fluid lost must be influenced by the state of the individual system, as well as by that of the surrounding medium. Thus, in the second experiment, Michael Griffiths lost 2 lbs. 6 oz., and Charles Cahell 2 lbs. 15 oz.; whilst in the third, Michael Griffiths lost 3 lbs., and Charles Cahell only 2 lbs. It is probable that the amount of liquid ingested not long previously might have a considerable influence on the quantity lost by transpiration under such circumstances. The most recent investigator into the conditions affecting the evaporation of fluid from the body is Erismann,* who examined them both in the dead and in the living body. In the *dead body* he found that the amount of fluid evaporating from a given area of the skin was the same whether the under surface was in contact with serum or with water, and whether the vessels were fully injected with water or not. The amount increased rapidly with temperature and with the dryness of the air, but it made little difference whether 1000 or 6000 litres of air passed over the surface in a given time. Evaporation took place most actively from those parts which contain the sweat-glands; the skin of the sole of the foot, for example, which contains, according to Krause, 2685 sweat-glands in the square inch, yielding nearly double the amount of insensible perspiration as compared with the skin of the belly, which has only 1136 in that area, notwithstanding the much greater thickness of the epithelium in the former situation. A dead body (the size of which is not given) of a woman lost 617·6 grains in 24 hours, the temperature being 63° F., and the amount of aqueous vapour in the air 64 per cent. (as compared with saturation). Experiments made upon the *living body* showed that the most important external factor in determining the amount of evaporation was the relative dryness or moisture of the air. Next came the temperature, and then the ventilation or amount of air blowing over the surface. The imbibition of a large quantity of hot fluid, by filling the vessels and increasing the pressure, augmented the evaporation. It was also increased by work, even though sweating did not occur. Considerable difference of opinion exists as to whether the insensible perspiration is discharged by the surface of the skin generally (Krause, Donders), or whether this is not the exclusive province of the sweat-glands. Erismann adduces many reasons in favour of the latter view, and it may at least be admitted that the greater part of the 'insensible' and all the 'sensible' perspiration is eliminated by these glands.

379. That the Cutaneous excretion is to a certain extent vicarious with the Urinary in regard to the amount of fluid eliminated, has been generally admitted, and is probably true; but the observations of Weyrich have shown that under similar conditions, avoiding extremes, both excretions rise and fall together, and that, consequently, no deductions can be drawn as to the amount of perspiration given-off from any estimates of the volume of urine discharged. We must not disregard the circumstance, however, that these two excretions are to a certain extent vicarious, in regard to the elimination of the products of the 'waste' of the system. Leube† has in particular shown that in certain affections of the kidneys the skin exudes urea, phosphoric acid, and chlorine in excess, whilst the quantity of these compounds appearing in the urine is correspondingly diminished. The share which the Skin has in this office has probably been generally underrated. As we have seen (§ 377), there is reason

* Erismann, 'Zur Physiologie der Wasserverdünstung von der Haut,' in the "Zeitschrift f. Biologie," Band xi. 1875, pp. 1–78.

† "Deutsche Archiv f. Klin. Med.," Band vii. p. 1.

to believe that a certain amount of azotized matter is excreted from it daily; and any cause which checks this excretion must throw additional labour on the kidneys, and will be likely to produce disorder of their function.—From the experiments of Aubert, it would appear that the proportion of Carbonic acid eliminated by the Skin is to that discharged by the Lungs as 1 : 200, whilst the amount of oxygen absorbed is as 1 : 180. Reinhard* estimates the daily amount of Carbonic Acid eliminated by the whole skin of an adult, by calculation from experiments made on one of his arms, at from 33 to 36 grains, and Röhrig found that the Skin of one arm yielded half a grain of Carbonic Acid gas per hour. The secreting action of the Skin is influenced by general conditions of the vascular and nervous systems, which are as yet ill understood. It is quite certain, however, that through the influence of the latter the secretion may be excited or suspended; this is seen on the one hand in the state of syncope, and in the effects of depressing emotions, especially fear, and its more aggravated condition, terror; and on the other, in the dry condition of the skin during states of high nervous excitement. It is possible that, in forms of fever, the suppression of the perspiration is a cause, as well as an effect, of disordered vascular action; for there are several morbid conditions of large parts of the surface, in which the suppression of the transpiration appears to be one of the chief sources of danger, having a tendency to produce congestion and inflammation of the internal organs. The operation of some poisons, like tobacco and jaborandi, induces copious sweating. From the experiments of Dr. Fourcault,† which have been confirmed by Valentin,‡ it appears that complete suppression of the perspiration in animals, by means of a varnish applied over the skin, gives rise to a state termed by him 'cutaneous asphyxia;' which is marked by imperfect arterialization of the blood, and considerable fall of temperature; which is probably the cause of death in the lower animals§. A partial suppression by the same means gives rise to febrile symptoms, and to albuminuria. Other symptoms that have been observed are tremors, hyperæsthesia, and subsequently anæsthesia of the skin, increased reflex excitability, tetanic cramps, movements of rotation of the whole body, paralysis of the bladder (Feinberg), ulcers in the stomach in consequence of extensive extravasations and diffuse parenchymatous inflammation of the kidneys (Socoloff).‖ In Valentin's experiments it was found that removal to a room of high temperature (71° to 140° Fahr.) was followed by remarkable temporary improvement in the condition of the animals, sensibility and voluntary motor power being reacquired, and in some instances food being taken. Death, however, always ultimately occurred. Laschkewitsch¶ regards the effects produced as analogous to those seen in paralysis of the vaso-motor nerves, where a hyperæmic condition of the vessels is present, and the animal loses heat rapidly, and more in proportion to the smallness of its size. He denies that the cause of death is asphyxia, but attributes it to cold, and refers in support of his view to the fact that death may be deferred or prevented by wrapping the animal in cotton wool. Lang** has pointed out that crystals of the triple phosphates which he attributes to the decomposition of urea may be found in all parts of the body after death

* "Zeits. für Biol.," 1869, p. 28.

† See his important Treatise, "Causes Générales des Maladies Chroniques," &c. 1844; and "Brit. and For. Med. Rev.," vol. xx. pp. 106–108.

‡ "Archiv für Physiolog. Heilk.," Band ii. 1858, p. 433.

§ Lomikowsky, Robin's "Journal de l'Anatomie," 1878, p. 468.

‖ Socoloff, "Centralblatt," 1872, p. 688. ¶ Reichert's "Archiv," 1868, p. 61.

** "Archiv d. Heilkunde," 1872, Band xiii. p. 277.

by suppression of the perspiration. He considers the animals die from uræmic poisoning. Feinberg,* on the other hand, refers the symptoms to the irritation of the cutaneous nerves caused by the stiffening of the varnish, which leads to vascular disturbances and paralysis, and secondarily to an affection of the spinal cord. The poisonous nature of the cutaneous secretion is well shown in an experiment made by Rohrig,† who found that the injection at noon of $3\frac{1}{2}$ ccm. of fresh filtered human sweat into the external jugular vein of a rabbit caused the temperature to rise from 99·2° F. to 104·3° during the evening, whilst the pulse rose from 192 per minute to 326, and the respiration from 82 to 105. On the following morning, the temperature remaining the same, the cardiac beats were 315, and the respirations 215 in the minute; after that it gradually returned to the normal in the course of the day. During the febrile state the urine contained albumin. There can be no doubt whatever, that imperfect action of the Cutaneous glandulæ, consequent upon inactive habits of life and want of ablution, is a very frequent source of disorder of the general system; occasioning the accumulation of that decomposing organic matter in the blood, which it is the special office of these glandulæ to eliminate. Hence the due maintenance of health requires that this excretion should be promoted by the use of the natural and appropriate means just referred-to; and this is the more necessary, when from any cause the function of the kidneys is imperfectly performed. There are many diseased states, moreover, in which there appears to be a special determination of the *materies morbi* to the Skin; and in which, therefore, the use of means that promote the cutaneous excretion constitutes the most efficient method of eliminating it from the blood.‡

CHAPTER XII.

EVOLUTION OF HEAT, LIGHT, AND ELECTRICITY.

1. *General Considerations.*

380. The series of Nutritive operations which has now been passed in review has been shown to consist in the continual appropriation, by the Animal organism, of certain 'organic compounds' or 'alimentary materials,' which have been generated for its use by Plants; and in the constant restoration of their elements to the Inorganic world, either in the very same forms of combination in which they originally existed there, or as products of incipient decay, by whose further decomposition those simple binary compounds will be reproduced. And thus, so far as the material components of the Organic Creation are concerned, the agency of of vegetable life is employed in withdrawing them from the Mineral world, and that of Animal life in returning them to it, after they have served their purpose in the living structure. But if we examine into the source of those active powers or 'forces,' on whose

* "Centralblatt f. d. Med. Wiss.," 1873, p. 545.

† 'Beiträge zur Physiologie der Haut,' "Jahrb. f. Balneologie," 1873, Band i. p. 1.

‡ The practical value of active diaphoresis in many febrile diseases, is well understood by the native practitioners among the Negroes of the Guinea Coast; who, according to Dr. Daniell ("Medical Topography and Native Diseases of the Gulf of Guinea," pp. 119–20), make use of it most successfully in the treatment of adynamic remittent fevers. Dr. Daniell states that having himself had abundant experience of its efficacy, he has no doubt of its superiority in these cases to the ordinary practice of venesection, saline purgatives, large doses of calomel, &c. And he has repeatedly stated that one great secret of preserving health in tropical climates, lies in due attention to the cutaneous functions.

operation every change, no less in the organized body, than in what is commonly designated as 'inert' matter, is dependent, we shall find that they are all traceable to the solar radiations. It is by the action of the Light and Heat of the Sun upon the Vegetable germ, that it is enabled to exercise its wonderful transforming capacity, whereby it extracts carbon, hydrogen, nitrogen, and oxygen, from the carbonic acid, water, and ammonia furnished by the atmosphere or the soil; and that it converts these into the albuminous, saccharine, and oleaginous compounds, which are the destined food of Animals.* And it is under the influence of Heat chiefly derived from the same source, that the greater number of tribes of Animals are enabled to apply these compounds to the purposes of organization; and that, through the peculiar instruments thus constructed, those various kinds of *Vital Force* are evolved, whose operations are so different from any which we witness in the Inorganic world. Accordingly we observe that the 'rate of life' in this larger proportion of the Animal Kingdom, is regulated, as in Plants, by the amount of Heat supplied to the organism from external sources; and that, when the external temperature is reduced below a certain point, there is an entire cessation of all vital activity. But there are certain tribes, especially Birds and Mammals, which possess the power of generating *Heat* within themselves, to such a degree as to render the rate of their vital processes almost entirely independent of external influences; and there is probably no one species that can exercise this power more effectually, and through a greater range of external conditions, than Man is able to do. Of this we shall presently have evidence.—The evolution of *Light*, again, is by no means an unusual phenomenon among the lower tribes of Animals; but where it does occur, it usually appears to have some special purpose, as is obvious enough in the case of the glow-worm and other luminous Insects. But the luminosity which is occasionally exhibited in Man must be regarded as an altogether abnormal phenomenon, whose physiological interest arises out of the peculiarity of the circumstances under which it presents itself.—Of the degree in which *Electricity* is generated in the living body, we know comparatively little. There can be no doubt that a disturbance of Electric polarity takes place in every action of Organic as well as of Inorganic Chemistry: and that every molecular change in the Animal as well as in the Vegetable organism must involve an alteration in its electric condition. But it would seem that in the Animal body generally, these alterations are made to balance each other so exactly, that no considerable disturbance of the electric equilibrium ordinarily takes place in the organism as a whole; and it is only in certain peculiar cases (as in the Electric Fishes) that a provision exists for the generation of Electricity in considerable amount and intensity, with a view to some special purpose. In the Human subject, however, an extraordinary production of free electricity, as of Light, occasionally presents itself; and this, taken in connection with other evidence, would seem rather to indicate a departure from the *balance* usually maintained between the opposite electrical changes continually taking place, than to be due to the introduction of any extraordinary sources of electric disturbance.

2. *Evolution of Heat.*

381. All the vital actions of the body of Man, as of that of 'warm-blooded' animals generally, require an elevated temperature as a condition of their performance; and the high degree of constancy and regularity which is observable in these actions, appears to depend in great degree upon the provision which the organism contains within itself, for the maintenance of that tempera-

* See Engelmann, Pflüger's "Archiv," Band xix. 1879, p. 1.

ture at a fixed standard. This constancy and regularity are most remarkably exhibited in the various *periodical* changes to which the body is subject both in health and in disease; the uniformity of whose recurrence is due to a corresponding uniformity in the rate of vital action taking place in the interval. Thus, as will be shown hereafter, the period of parturition is in great degree determined by the maturation of the fœtal structures; and the uniformity of the time which this requires (like the corresponding uniformity in the period of development in the embryo-bird) may be fairly attributed to the regularity of the supply of Heat, which is the power that especially determines the formative operations. For the periods of all similar phenomena in 'cold-blooded' animals, which have comparatively but feeble power of maintaining an independent temperature, exhibit no such uniformity; yet even in the lowest Vertebrata, according to Mr. Gulliver,* the temperature of the body is from 2° to 5° warmer than that of the medium in which they live. Heat, which is a mode of motion, is generated whenever stronger chemical affinities than those which were previously in action are satisfied; hence the temperature rises in muscles that are made to contract, and in glands when they are in the active performance of their function. The liver, spleen, kidneys, and glands of the intestinal tube,† with the brain,‡ the muscles during exercise, and the blood§ itself are the chief generators of heat in the body, because in all these parts active processes of oxidation are taking place by which the constituents of these organs and tissues are reduced to lower and more stable planes of composition leading to a certain amount of force being set free in the form of heat. We shall now inquire, in the first place, into the amount of heat thus generated by Man; and then into the sources of its production.

382. Our present knowledge of the ordinary Temperature of the Human Body, under different circumstances, is due to the investigations of a multitude of observers, references to many of which will be found in Wunderlich's exhaustive treatise.‖ A series of observations made by Dr. J. Davy¶ included 114 individuals of both sexes, of different ages, and among various races and different latitudes, and under various temperatures; the external temperature, however, was in no instance very low, and the variations were by no means extreme. The mean of the ages of all the individuals was 27 years. The following is a general statement of the results, the temperature of the body having been ascertained by a thermometer placed under the tongue:—

Temperature of the air	60°	Average temperature of the body	98·28°
,, ,,	69°	,, ,, ,,	98·15°
,, ,,	78°	,, ,, ,,	98·85°
,, ,,	79·5°	,, ,, ,,	99·21°
,, ,,	80°	,, ,, ,,	99·67°
,, ,,	82°	,, ,, ,,	99·9°
Mean of all the experiments . .	74°	Mean of all the experiments . .	100°
Highest temperature of air . . .	82°	Highest temperature of body .	102°
Lowest temperature of air . . .	60°	Lowest temperature of body . .	96·5°

* Lecture IX., "Med. Times and Gaz.," Jan. 17th, 1863.

† See Winternitz, in Stricker's "Med. Jahrbücher," 1871, p. 180.

‡ Heidenhain, Pflüger's "Archiv," Band iii. p. 504. Funke, "Physiologie," 1873, p. 306.

§ See Gamgee, on 'Heat Generated in the Blood during Arterialisation,' "Brit. Assoc. Reports," 1871. Bernard, "Chaleur Animal in Revue Scientifique for 1872."

‖ Wunderlich's treatise has been translated by Dr. Woodman for the New Syd. Society. See also Brown-Séquard ("Journal de la Physiologie," 1859, p. 549), whose experiments essentially corroborate those of Dr. Davy, as well as the older ones of MM. Eydoux and Souleyet ("Comptes Rendus," 1838, p. 457), except that he found a greater difference in the temperature of the men he examined, though the variation of the atmospheric temperature was much less. E. Oertmann (Pflüger's "Archiv," Band xvi. 1878, p. 101) has lately suggested the introduction of the thermometer into the stream of urine escaping from the urethra during micturition, as a rapid means of ascertaining the temperature of the interior of the body with accuracy.

¶ See "Anatomical and Physiological Researches."

From this we see that the variations noted by Dr. Davy, which were evidently in part the consequence of variations in external temperature, but which were also partly attributable to individual peculiarities, amounted to $5\frac{1}{2}$ degrees; the lower extreme might be found to undergo still further depression, if the inquiries were carried on in very cold climates. Wunderlich* gives as the result of the numerous observations made by himself and others of late years, a lower mean temperature than Dr. Davy, and states that the range of normal temperature in the axilla is from 97·25° Fahr. to 99·5° F., and that the *mean normal temperature* is 98·6° F. Climate appears to have very little influence on the temperature of the healthy adult white man. Hence a much larger absolute amount of heat must be generated in the body in cold climates and with low external temperatures.† The temperature of the natives of India is said to be a little higher than the mean.‡ It is also higher in Icelanders,§ whilst it is as much as 2·5° F. lower in Africans.‖ It is slightly higher in women. A slight increase occurs during the last two months of pregnancy,¶ and an augmentation of 0·3° F. has been observed *during* labour pains. Amongst the most important of these variations that occur in the temperature of the body are those dependent upon Age, Period of the Day, Exercise or Repose, Ingestion of Food or Drink, and External Temperature.

1. The temperature of *Infants* just born, according to the observations of Andral, Dr. Davy, M. Roger,** and Dr. G. C. Holland,†† is somewhat higher than that of adults,‡‡ provided that they are placed in conditions favourable to its sustenance; but, as will be shown hereafter, infants and young children are very inferior to adults in their power of resisting the depressing influence of external cold. Their temperature before birth is a trifle higher than that of the mother's uterus or vagina.§§ When examined immediately after birth by a thermometer in the axilla, it is nearly 100°; but it quickly (2 hours‖‖) falls to about 95·5°, and gradually rises in the course of the next twenty-four hours to about 97·7° in weakly subjects, and to 99·5° in strong infants. Between four months and six years of age. M. Roger found the average temperature to be 98·9°; and, between six and fourteen years of age, 99·16°. Dr. Finlayson¶¶ states that from 300 observations made on children he satisfied himself that in them there was a minimum from about 10 P.M. to 3 A.M., a gradual rise during the early morning hours, a maximum during the day, and a tolerably rapid fall during the early part of the evening. The average range of temperature amounted to more than 3° Fahr., and this variation he believes cannot be explained by reference to the diurnal range in the temperature of the air, to the influence of daylight, of muscular exertion, of food,

* Loc. cit., p. 82.

† See Crosse Johnston, "Reports of the Army Med. Department," 1876; also J. P. Boileau, "Lancet," 1878, vol. i. p. 413; Thornley, "Lancet," 1878, vol. ii. p. 352; Finkler, Pflüger's "Archiv," Band xv. 1877, p. 603.

‡ See Crombie, "Indian Annals of Med. Science," No. xxxii.

§ Thomsen, "Ueber Krankheiten auf Island," &c., p. 24.

‖ Livingstone, "Travels in South Africa," p. 509.

¶ Beaunis' "Physiologie Humaine," p. 723. ** "Archiv. Gén. de Méd.," 1844.

†† "Inquiry into the Laws of Life," 1829.

‡‡ Dr. W. F. Edwards ("On the Influence of Physical Agents on Life," p. 115) gives as the result of his observations, which were only ten in number, that the temperature of infants is lower than that stated above; but it is obvious that these observations were made during the period of depression which occurs in the first few days, whilst the respiratory function is becoming established.

§§ Bärensprung, Müller's "Archiv," 1851. See also Andral, "Comptes Rendus," t. lxx. 1870, p. 825.

‖‖ Dr. J. Maclagan, "Transact. Roy. Soc. of Edinb.," 1870; abstract in "Lancet," Aug. 13th, 1870, p. 243. ¶¶ In a paper read before the Phil. Soc. of Glasgow, Dec. 3rd, 1873.

or of sleep, but is simply an expression of a law of daily periodicity affecting the body.*—The Temperature of *aged* persons, from the observations of Dr. J. Davy, does not seem to be below that of persons in the vigour of life, provided that there be no external depressing influences; but they seem, like infants and young children, to have less power of resisting external cold, the temperature of their bodies being more easily and considerably reduced by it than is that of adults; and hence probably it has happened that popular opinion assigns to them an habitually inferior temperature.

II. A slight *diurnal* variation in the temperature of the body appears usually to take place, quite irrespectively of external heat or cold; but this does not seem to be very constant either in its period or its degree, and is seldom very considerable. The concurrent observations of many observers show† that the body is warmer in the morning and colder at night. Dr. Ogle found that the temperature rose from morning till late in the afternoon, after which it fell till bedtime. The lowest temperature occurred about daybreak. The average diurnal variation was about 1·5° Fahr. The minimum temperature noticed was 97° at 5.30 A.M., in winter. The maximum was 100·6° whilst in a Turkish bath of 120°. The extreme oscillation of temperature, therefore, was not more than 3·5° F. in health. Dr. Jürgensen found the diurnal variation to amount to from 1·8° to 3·6° F.; the minimum occurred from 1.30 A.M. to 7.30. The temperature then, with some fluctuation, rose till 4 P.M., when it attained its maximum, which lasted till 9 P.M., and after this it again fell. Dr. Casey found his mean temperature during the day to be 98·07 F., the mean range of temperature 1·61° F. The maximum range 2·5°. The maximum temperature was at 7.30 P.M. Sidney Ringer and P. Stewart give the average maximum temperature for persons under twenty-five years of age at 99·1° F., of those over forty 98·8° F. They find the period of highest temperature extends from 9 A.M. till 6 P.M.; the lowest is about midnight. These observations correspond well with what has already been pointed out with regard to the relative activity of the respiration (§ 287, VIII. and IX.), and circulation at different periods of the twenty-four hours. As a rule the temperature of the two sides of the body is alike, but Blake‡ has observed that the right side is sometimes as much as 1° F. higher than the left during exertion, especially in the sun.

III. That an increase in the heat of the body is produced by *exercise*, and that repose tends to its reduction, is a matter of familiar experience; but the observations of Dr. Davy show that there is scarcely any perceptible difference in the heat of the deep-seated parts, the augmentation and depression being confined to the extremities. Thus, on one occasion recorded by him, the temperature of the air of the room before walking being 60°, that of the feet (shown by a thermometer placed between the toes) being only 66°, that of the thermometer under the tongue being 98°, and that of the urine being 100°, —the temperature after a walk in the open air at 40°, the exercise having diffused a feeling of gentle warmth through the body, was 96·5° in the

* Sitz ("Jahrb. f. Kind.-heilk.," Band iv. 1871, p. 414) is in accord with Finlayson.

† Davy, loc. cit., W. Ogle, "St. George's Hospital Reports," vol. i. p. 221. Dr. Ogle's experiments were made on two healthy adults; the temperature being taken by introducing a warmed self-registering thermometer three or four times a day under the tongue, and retaining it in that position for several minutes. They extended over a year. Jürgensen, "Deutsches Archiv f. Klin. Med.," Band iii. p. 166. Dr. Jürgensen's experiments extended over three days, and consisted in reading off at intervals of five minutes the indications of a thermometer permanently retained in the rectum at a depth of about two inches. Casey, "Lancet," vol. i. 1873, p. 200. See also Ringer, "Proceed. of the Roy. Soc.," vol. xvii. p. 287.

‡ E. Blake, "Med. Times and Gazette," Oct. 1871.

feet, 97° in the hands, 98° under the tongue, and 101° in the urine. So, on another occasion, the temperature having been 66° in the room, 75° in the feet, 81° in the hands, 98° under the tongue, and 100° in the urine,—after a walk in air at 50° the temperature was 99° in the feet, 98° in the hands, 98° under the tongue, and 101·5° in the urine. These effects are, therefore, in all probability, chiefly due to an increase in the energy and frequency of the heart's contractions, by which means the warm blood is driven with greater velocity through the extreme capillaries, imparting its heat to the surrounding parts. Marcet* found in the ascent of Mont Blanc that when at rest the temperature of the body did not vary very much at different heights. In the ascent, as Lortet† observed, the internal temperature of the body fell during exercise, especially when the stomach was empty and the skin was freely perspiring—to a degree, indeed, that was almost proportional to the height ascended. When the feeling of malaise, so often complained of by Alpine travellers, or *mal de montagne*, was most evident, the temperature was lowest, and the sensation was best removed and the temperature raised by frequent ingestion of food. The observations of Clifford Allbutt‡ do not support the statements of Lortet, for he found that, with one or two exceptions, the tendency of exercise in Alpine climbing was to elevate the temperature. The forenoon rise occurred earlier, and the evening fall had often reached the night-level at 9 P.M. The difference was probably owing to the different physique of the two observers. Passive movement (swinging or rocking for fifteen minutes) was found by Manassein§ to lower the temperature of rabbits about 1° Fahr., even when they were carefully protected from draught. The depression reached its maximum half an hour after the swinging had ceased, and lasted for two hours. The experiments of various observers, moreover, have shown that a certain amount of heat is developed during the active contraction of muscular tissue, the rise in temperature of a muscle like the Biceps, after a few powerful contractions, being as much as 1° Fahr.; and this increase in temperature may be regarded as due to the increased energy of the chemical changes, and in some measure also to the mechanical effects of friction, &c., taking place in the contracting muscle.‖ It is remarkable that voluntary increase of the frequency and extent of the respiratory movements for the space of ten minutes, or suspension of the respiration at the end of a full inspiration, alike produce a decline in the temperature of the blood, as shown by that of the skin over the radial artery; in the former case amounting, in M. Lombard's¶ experiments, to as much as 2° Fahr. Drs. Wilson Philip, Hastings, and C. J. B. Williams have pointed out that here, just as in the performance of artificial respiration, the cooling effect of the air introduced is greater than the warming effect of the respiratory processes to which it becomes subservient. Coincidentally with such increase of the respiratory movements, however, there is diminution of the force and tension of the pulse, as shown by the sphygmograph, which may to some extent explain the fall. It thus appears that the temperature of the body is not raised by exercise to the extent that might be expected, its increase beyond a certain point being provided for by more rapid breathing, the quicker circulation of the blood through the skin, and consequently quicker cooling by radiation, sweating, &c., so that, as Wunderlich observes, the opposing condi-

* "Archiv. des Sci. Physiques," t. xxxvi. p. 247. † "Centralblatt," 1869, p. 781.
‡ "Journal of Anatomy and Physiology," 1873, vol. vii. p. 117.
§ Pflüger's "Archiv," Band iv. 1871, p. 283.
‖ See Fick, Pflüger's "Archiv," Band xvi. p. 59, 1878.
¶ Brown-Séquard "Archives de Physiologie," t. i. 1868, p. 479.

tions of the loss of force by mechanical work and by quicker cooling, and on the other hand the overplus through augmented chemical action, compensate each other in health, *and the final difference of temperature during rest and during labour* is extremely trifling.

IV. The influence of *ingestion of food* upon the temperature of the body was found, in Dr. Ogle's and in Dr. Jürgensen's experiments, to cause a slight elevation of the temperature both of the mouth and of the rectum, unless wine were consumed, when a decline occurred. Dr. Jürgensen observed no change beyond a slight depression of the mean diurnal temperature after fasting for 26 hours; but when the abstinence was prolonged to a period of 62 hours, the mean diurnal temperature rose, and the usual period of depression did not occur. Drs. Ringer and Rickards* have shown that, excepting in those who are much accustomed to its use, the ingestion of alcohol in considerable doses causes a remarkable diminution of temperature, amounting in some cases to about 3° F. In rabbits, the injection of alcohol into the rectum caused a depression of the animal heat amounting to 15°. They found that alcohol in various doses produces only slight and temporary depression of the temperature of febrile persons; and consequently, that although when indicated, it will act to some extent beneficially in virtue of its power to cause some diminution of the temperature, yet it cannot bring the temperature of febrile persons to that of health. The experiments of Dr. W. Ogle,† and of Tscheschichin,‡ are confirmatory of the preceding results. Dr. Ogle found that tea caused an elevation of temperature. Common experience leads to the conclusion that after a meal, as after exercise, there is greater warmth in the extremities; but Dr. Davy's observations show that, in his own person, whilst resident in England, there was usually an appreciable depression immediately after dinner, though in Barbadoes the effect of a moderate meal was to produce an elevation. In both cases, however, Dr. Davy observed that the ingestion of *wine* had a positively-depressing influence on the temperature of the body, which increased with the quantity taken; and it may have been the constant employment of wine with his dinner which was the real cause of the depression observed in England.

V. The influence of *external temperature* is sufficiently apparent in the observations already cited; for although external cold may act in a different degree on different individuals, according to their respective ages, powers of resistance, &c.; sometimes, when its action is brief, causing a slight increase of temperature; yet there is ample proof that on the whole a continued exposure to it reduces the temperature of the body somewhat below its ordinary standard, whilst continued exposure to heat occasions a slight elevation in the temperature of the body. The influence of cold is, of course, most powerfully exerted when the body is at rest; and under such circumstances Dr. Davy found the temperature of his own body to be reduced, on an average of four observations, to 96·7° F., the average temperature of the surrounding air having been 37° F. On comparing the bodily temperature of different individuals working in rooms of various temperatures in the same factory, Dr. Davy found the tongue-thermometer rise to 100° F. in one man, and to 100·5° in another who had been working for some hours in a room at 92°; whilst it was 99° in a young woman who worked in a room at 73°, and only 97·5° in another who worked in a temperature of 60°. Dr. Schuster§ found the effects of baths of different kinds, as hot water and douche baths, was to cause an elevation of temperature, and to increase the rapidity of the pulse. Horvath, in experiments on

* "Proceed. of the Roy. Med.-Chir. Soc.," vol. v. 1866, p. 209. † Op. cit., p. 238.
‡ Reichert's "Archiv," 1866, p. 151. § Virchow's "Archiv," Band xliii. p. 60, 1868.

rabbits, found that when they are cooled down by snow to 73° F. the heart beats rarely, excitation of the vagus is inoperative, the intestines are motionless and non-excitable, asphyxiation causes neither augmentation of the blood-pressure nor cramps, but all these phenomena are reversed when the temperature is raised to 100° F.* The lowest temperature to which Horvath† succeeded in cooling puppies with subsequent restoration was 40° F. as measured by a thermometer in the rectum. The effects of seasonal change are less marked in man than they are in the lower animals, which are more exposed to extremes of temperature; but it seems principally exerted in modifying the heat-producing power. For it has been shown by Dr. W. F. Edwards that warm-blooded animals are more speedily killed by extreme cold in summer than in winter; and it seems probable, therefore, that we are partly to attribute the peculiar chilling influence of a cold day in summer, and the oppressiveness of a warm day in winter, to the seasonal change in the body itself; although the effect is doubtless referable in part to the effect of contrast upon our own feelings.‡ Budge states that during the spring months the temperature of the body is a little higher than in winter.

383. The influence of the nervous system upon the temperature of the body presents some interesting features. Local variations of temperature are effected essentially through the vaso-motor nerves, which for the most part run in the sympathetic system. Speaking generally, it may be said that stimulation of the vaso-motor nerves of any part by contracting the capillaries and diminishing the supply of blood, occasions a reduction of temperature in it, whilst paralysis or division of the vaso-motor system, by causing dilatation of the capillaries, leads to a more rapid circulation and a higher temperature. In accordance with this the effects of section of the spinal cord are not constant, for such lesion is sometimes followed by an elevation, and sometimes by a decline in the temperature. Thus, a case is recorded by Sir B. Brodie§ in which the spinal cord having been so seriously injured in the lower part of the *cervical* region that the whole of the nerves passing off below were completely paralysed, the heat of the body, as shown by a thermometer placed in the groin, was not less than 111° F.; and this, notwithstanding that the respiratory function was very imperfectly performed, the number of respirations being considerably reduced, and the face livid. Similar cases have been recorded by other observers. On the other hand, when the spinal cord has been divided experimentally in animals, Sir B. Brodie‖ and others have shown that

* Horvath, "Wien. Akad.," 1870, No. 11. † "Centralblatt," 1871, p. 513.

‡ Many of the lower animals, as the Marmot and Dormouse, hybernate during the winter, and their state has been very carefully examined by Valentin and by Horvath ("Centralblatt," 1872, pp. 706, 721, and 737). Horvath's experiments were conducted on Marmots (Spermophilus citillus), which exist in large quantities in Russia. In captivity he finds that during the winter they sleep for about four days and then wake for four days. During the sleeping period they can be cooled down to such a degree that a thermometer introduced into the rectum to the depth of an inch and a half indicated only 3° F. above the freezing point. The temperature rose rapidly after the animal awoke, so that in the course of an hour it was 3° F. higher, at the close of the second hour 9° F. higher, and at the end of the next half hour about 27° F. The cause of this remarkable elevation of temperature is according to Horvath scarcely explicable on the ordinary chemical theory of calorification, since neither the respiration nor the muscular movements were correspondingly augmented.

§ "Med. Gaz.," June, 1836, and "Physiolog. Researches," p. 121.

‖ "Philosophical Trans.," 1811, 1812, and "Physiological Researches." See also the confirmatory experiments of MM. Le Gallois, "Annales de Chemie," 1817, and "Œuvres," t. ii. Chossat, "Mémoire sur l'Influence du Syst. Nerv. sur la Chaleur Animale;" and Tscheschichin, Reichert's "Archiv," 1866, pp. 151–179; Naunyn and Quincke, idem, 1869, pp. 174, 521. C. Bernard, "Comptes Rendus," 1853, t. xxxvi. pp. 414 and 632. Schiff, "Untersuchungen," Heft 3; "Physiol. d. Nerven-System," 1855. Fischer, "Centralblatt

the temperature of the body usually falls with rapidity, even when artificial respiration is steadily maintained. This difference, however, is probably due to the secondary conditions of the experiment, for it is to be particularly noted that section of the cervical region of the spinal cord, providing peripheral cooling be prevented by suitable means, is followed by a marked rise of temperature, whilst division of the dorsal region of the cord is followed by depression of temperature. No rise of temperature occurs in the former case if the anterior columns be spared. Hence Fischer contended that an inhibitory or regulating centre for heat exists in the anterior columns of the cervical portions of the cord, stimulation of which caused depression, and paralysis of which was followed by increase of the body temperature. Erb considers it most reasonable to assume that in these experimental lesions there is a paralysis of certain parts which serve to restrict the production of heat. At the same time, however, an extensive vascular paralysis takes place, whereby an increased amount of heat is given off, which more or less compensates for the increased production. According to the preponderance of one or the other factor, the rise of temperature will be more or less considerable, or may be absent or even be a minus quantity. In M. Tscheschichin's experiments, section of the pneumogastrics was not observed to produce any remarkable effect upon the development or distribution of the animal heat in rabbits—at least not until those pathological conditions which have been already described (§ 282), as resulting from their section, had become established. Various pathological phenomena indicate that the withdrawal of nervous influence from any part of the body usually tends to produce a depression of its temperature, and this especially in the extremities; thus Mr. H. Earle* found the temperature of paralysed limbs slightly lower than that of sound limbs; so Prof. Dunglison has noticed that in one case of hemiplegia of five months' standing, the temperature of the axilla was 96½° on the sound side, and 96° on the paralysed; whilst that of the hand was 87° on the sound side, and only 79½° on the paralysed; and in another case of only a fortnight's duration, the temperature of the axilla was 100° on the sound side, and only 98¼° on the paralysed, whilst that of the hand was 94° on the sound side, and 90° on the paralysed.† According to Folet,‡ the temperature of the paralysed side soon after an attack of hemiplegia is 1·8 Fahr. above that of the opposite side; but, when atrophy supervenes, the temperature falls again. The elevation is quite independent of the seat of the lesion of the nervous system.

384. The usual temperature of the body occasionally undergoes considerable alteration in *disease;* and this in the way either of increase or of diminution. Thus in maladies which involve an acceleration of pulse and a quickening of the respiration, the temperature is generally higher than usual, even though a large portion of the lung may be unfit for its function. This is often remarkably seen in the last stages of phthisis, when the inspirations are extremely rapid,

f. d. Med. Wiss.," 1869, p. 259. Brown-Séquard, "Revue Scientif.," 1871, p. 288. The remarkable case recorded by Hutchinson, "Lancet," 1875, vol. i. p. 713; and that by Dr. Teale, already referred to. Heidenhain in Pflüger's "Archiv," Band iii. p. 504; and Weir Mitchell, Brown-Séquard's "Archives of Scient. and Pract. Med.," 1873, No. 4. Schreiber, Pflüger's "Archiv," Band viii. 1874, p. 576. Erb, Ziemssen's "Cyclopæd. of Pract. Med.," Amer. edit., vol. xii. p. 128, 1878. C. V. Schroff ("Centralblatt für die Med. Wiss.," 1877, p. 38) found that on dividing the spinal cord of a dog at the level of the seventh cervical vertebra, and enveloping the animal in wool, there was a fall of temperature during the first hour, amounting to 0°·6 C. A rise of 2°·9 C. occurred in the course of the next five or six hours, which was followed by a gradual fall coinciding with great acceleration of the respirations.

* "Med.-Chir. Trans.," vol. vii. † "Human Physiology," 7th edit., vol. ii. p. 238.

‡ "Gaz. Hebdomad.," 1867, Nos. 12–14. See Adae, "Centralblatt f. d. Med. Wiss.," 1877, p. 86. Nieder, "Med. Times and Gazette," 1873, No. 1180.

and the pulse so quick as scarcely to admit of being counted; the skin, in such cases, often becomes almost painfully hot. On the other hand, in diseases of the contrary character, such as "morbus cœruleus," asthma, and cholera, the temperature of the body falls; a very considerable reduction of temperature having been noticed in both maladies. The range observed by M. Andral in diseases which less affected the calorifying function, was from 95° to 107·6°; and by M. Roger (loc. cit.), in diseases of children, from 74·3 to 108·5. Professor Dunglison* speaks of having seen the thermometer at 106° in scarlatina and typhus; and Dr. Francis Home† found it to stand at 104° in two individuals in the cold stage of an intermittent, whilst it afterwards fell to 101°, and subsequently to 99°, during the sweating stage. Dr. Edwards mentions a case of tetanus, in which the temperature of the body rose to 110¾°. The following observations have been made on this subject by M. Donné:‡ in a case of puerperal fever, the pulse being 168, and the respirations 48 per minute, the temperature was 104°; in a case of hypertrophy of the heart, the pulse being 150, and the respirations 34, the temperature was 103°; in a case of typhoid fever, the pulse being 136, and the respirations 50, the temperature was 104°; and in a case of phthisis, the pulse being 140, and the respirations 62, the temperature was 102; on the other hand, in a case of jaundice, in which the pulse was but 52, the temperature was only 96·4°; but the same temperature was observed in a case of diabetes, in which the pulse was 84. These limited observations, whilst they clearly indicate that a *general* relation exists between the temperature of the body and the rapidity of the pulse, also show that this relation is by no means invariable, but that it is liable to be affected by several causes, of which our knowledge is as yet very slight. Persistent high temperature of the body (105°–110°) in febrile affections usually indicates a fatal issue. The highest temperature yet observed has been reported by Dr. J. Teale, of Scarborough, who in a case of injury to the spine from a fall registered the remarkable temperature of 122° Fahr., the pulse being 120.§ In this instance the patient recovered.‖ Jacobson,¶ from experiments made with thermo-electric instruments, has satisfied himself that the temperature of intensely inflamed skin and muscles never rises so high as the temperature of the inner parts of the body, which is quite in accordance with the dictum of John Hunter, that local inflammation cannot raise the temperature higher than the degree of warmth found at the centre of the circulation. It is still doubtful whether the augmented temperature observed in febrile diseases is due to diminished elimination or to increased production of heat, but considering the large excess of heat that is developed during the crisis of fevers there seems to be reason for believing that Leyden's view in favour of excessive production of heat is correct.** It is not a little remarkable that the temperature of the body should frequently *rise* considerably *after death;* and this not merely in such cases as Cholera, in which it has undergone an extreme depression during the latter part of life; but even in the case of febrile disorders, in which the temperature during life has been above the usual standard. This has been ascertained

* "Human Physiology," 7th edit. vol. ii. p. 225.

† "Medical Facts and Experiments," London, 1759.

‡ "Archiv. Gén. de Méd.," October, 1835.

§ "Lancet," March 6th, 1875.

‖ According to Lewitzky the febrile condition that follows the injection of putrid fluids into the blood is not due to the Bacteria that are present in such fluid. "Centralblatt," 1873, p. 723; see also Naunyn, abstract in idem, p. 731; and Burdon Sanderson, "Brit. Med. Journ.," January 1878.

¶ Virchow's "Archiv," Band li. Heft 2.

** See Milner Fothergill's Paper read before the Medical Society of London, pamphlet, 1873.

by Dr. Bennet Dowler,* of New Orleans, on the bodies of those yellow-fever subjects which may be especially referred to as exhibiting a remarkable degree of *molecular* life after *somatic* death. In one case, for example, the highest temperature during life was in the axilla, 104°; ten minutes after death, it had risen to 109° in the axilla; fifteen minutes afterwards, it was 113° in an incision in the thigh; in twenty minutes, the liver gave 112°; in one hour and forty minutes, the heart gave 109°, and the thigh in the former incision 109°; and in three hours after the removal of all the viscera, a new incision in the thigh gave 110°. It is curious that the maximum heat observed after death should have been in the thigh, and the minimum in the brain. The post-mortem rise in temperature appears to be esssentially due to the passage of the muscles of the body into the state of rigor mortis, a change that is associated with chemical action analogous to that occurring during contraction, and accompanied by a corresponding elevation of temperature.† Ackermann has pointed out that the post-mortem rise may in part be due to the persistence of the heat-producing chemical changes in the deeper parts of the body, whilst the radiation and loss of heat from the surface by evaporation is reduced by the contraction of the cutaneous vessels and the cessation of the circulation, and Wunderlich suggests that it may be also in some measure owing to the paralysis of that part of the nervous system which inhibits or regulates the generation of heat, supposing such centre to enist.

385. Although there appears to be, for all kinds of animals, a distinct limit to the variations of bodily temperature, under which their vital operations can be carried on, this limitation does not prevent certain species from existing in the midst of great diversities of external conditions; since they have within themselves the power of compensating for these, in a very extraordinary degree. This power seems to exist in Man to a higher amount than in most other animals; since he can not only support, but enjoy life, under extremes of which either would be fatal to many. In some parts of the tropical zone, the thermometer rises every day, through a large portion of the year, to 110°; and in British India it is said to be seen occasionally at 130°. On the other hand, the degree of cold frequently sustained by Arctic voyagers, and quite endurable under proper precautions, appears much more astonishing; by Captain Parry the thermometer has been seen as low as −55°, or 87° below the freezing-point; by Captain Franklin at −58°, or 90° below the freezing-point; and by Captain Back at −70°, or 102° below the freezing-point. In both cases, the effect of the atmospheric temperature on the body is greatly influenced by the condition of the air as to motion or rest: thus, every one has heard of the almost unbearable oppressiveness of the 'sirocco' or hot wind of Sicily and Italy, the actual temperature of which is not higher than has often been experienced without any great discomfort when the air is calm; and on the other side, it may be mentioned that, in the experience of many Arctic voyagers, a temperature of −50° may be sustained, when the air is perfectly still, with less inconvenience than is caused by the air in motion at a temperature 50° higher.‡ This is quite conformable to what might be anticipated on physical principles.

* "Western Journal of Medicine and Surgery," June and Oct. 1844; cited in "Philadelphia Medical Examiner," June 1845, and in Prof. Dunglison's "Human Physiology," 7th edit. vol. ii. p. 718.

† See the papers of Walther, "Centralblatt für die Med. Wiss.," 1867, p. 391; Wunderlich, "Archiv d. Heilkunde," Band v. p. 205; Huppert, idem, Band viii. p. 321; Fick and Dybkowsky, "Vierteljahrschrift d. Zurich Naturf. Gesellsch.," 1867; Ackermann, "Deutsche Archiv f. Klin. Med.," Band ii. p. 359; Valentin, "Post-mort. Temp.-steigerung Dissert." Leipzig, 1869.

‡ The Author has been informed by Sir John Richardson, that in his last Arctic Expedition,

386. Again, the degree of *moisture* contained in a heated atmosphere, makes a great difference in the degree of elevation of temperature which may be sustained without inconvenience. Many instances are on record of a heat of from 250° to 280° being endured in *dry* air for a considerable length of time, even by persons unaccustomed to a particularly high temperature; and persons whose occupations are such as to require it, can sustain a much higher degree of heat, though not perhaps for any long period. The workmen of the late Sir F. Chantrey were accustomed to enter a furnace in which his moulds were dried, whilst the floor was red-hot, and a thermometer in the air stood at 350°; and Chabert the "Fire-king" was in the habit of entering an oven the temperature of which was from 400° to 600°.* It is possible that these feats might be easily matched by many workmen who are habitually exposed to high temperatures; such as those employed in Iron-foundries, Glass-houses, and Gas-works. In all these instances, the dryness of the air facilitates the rapid vaporization of the fluid, whose secretion by the Cutaneous glandulæ is promoted by heat applied to the surface; and the large amount of caloric which is consumed in this change, is for the most part withdrawn from the body, the temperature of which is thus kept down. By some experimenters, as by Ackermann,† an attempt has been made to show that the lungs as well as the skin constitute a regulating mechanism for preserving an equality of the temperature in warm-blooded animals; since if an animal be exposed to a gradually increasing temperature its temperature rises, but its respirations also increase in number, quite apart from the deficiency of oxygen or increase of carbonic acid in the blood, and ultimately a form of dyspnœa is produced, due simply to heat.‡ The increased number of respirations on exposure to warm air does not, according to Riegel,§ occur in rabbits and dogs in which the spinal cord has been divided high up, and the temperature of the animal continues to rise. In Riegel's experiments on animals under the influence of curare, and in which artificial respiration was maintained, all conditions of the experiment remaining the same, the temperature invariably fell in proportion as respiration was quickened. It is difficult to say whether the power of generating heat which the body possesses is capable of being self-regulated or governed in conformity with the external conditions that may at any time be present; that is to say, whether when the body is exposed to cold more heat is produced, and when to heat, less.

whilst at winter-quarters, he was accustomed to go from his sitting-room to the magnetic observatory at a short distance (about an ordinary street's breadth), without feeling it necessary even to put on a great-coat; although the temperature of the former was about 50°, and that of the air through which he had to pass to the latter was −50°, the difference being 100°. This immunity from chilling influence was chiefly attributable to the *dryness* and *stillness* of the atmosphere; but it is worthy of note that Sir J. Richardson and the whole of his party on this expedition, abstained entirely from alcoholic liquors; and the Author has received his personal assurance that his experience on this occasion fully bore out his previous conviction, that continued severe cold is *much better* borne without recourse to these stimulants than under the employment of them.

* The wonderful feats performed by many individuals from time to time—of dipping the hand into melted lead, laying hold of a red-hot iron, &c.—have been recently shown by M. de Boutigny to be explicable upon very simple principles. For in all such cases a thin film of aqueous fluid in the 'spheroidal state' intervenes between the skin and the heated surface; and a hand which is naturally damp, or which has been slightly moistened, may be safely passed into the stream of *molten iron* as it flows from the furnace; as was demonstrated by M. de Boutigny at the meeting of the British Association at Ipswich in 1851.

† "Archiv f. Klin. Med.," Band ii. p. 361. See Woodman's Abst. of Riegel's Paper in "Lond. Med. Record," 1874, p. 744.

‡ See also Fick and Goldstein, 'Ueber Warmdyspnœa,' "Inaug. Abhand.," Würzburg. Verhand., 1871.

§ Virchow's "Archiv," Band lxi. Heft 3.

Liebermeister* found that in a cold bath, or on exposure of the surface to cool air (54°—70° F.), the temperature of the interior of the body in the first instance rose slightly or remained stationary, though it fell after long immersion or exposure. It fell also after removal from the cooling influence. This he explained by considering that the body possesses the power of generating more heat when required, though this power is limited; whilst the secondary fall, when there is no longer any withdrawal of heat, is due to the cooling of the blood circulating in the capillaries of the cool skin. Kering† endeavoured to furnish a further proof by showing that with increase of external heat, or by preventing the body from losing its temperature, a diminished production of heat takes place. Jürgensen‡ and Senator§ oppose these statements, and maintain that when the body is exposed to cold, there is no increased production of heat, but the superficial vessels contract, and a badly-conducting superficial layer of tissue exists, so that the blood in the deeper organs is prevented from giving off its heat, and thus with unaltered production of heat may rise in temperature. As soon as the exposure to cold ceases, the cutaneous vessels dilate, and the blood circulating through the cooled part leads to a fall of temperature. Funke‖ considers that the rapid rise that occurs in the temperature of the body in animals that have been thoroughly cooled, when placed under favourable circumstances, is in favour of Liebermeister and Kering's views. Exposure to intense cold causes a fall of the temperature of the whole body from the first, and *vice versâ* during exposure to a hot bath.¶

387. Exposure to a very elevated temperature, if continued for a sufficient length of time, does produce a certain elevation of that of the body; as might be expected from the statements already made in regard to the variation in the heat of the body with changes in atmospheric temperature (§ 382). Immersion in a hot bath, at the temperature of the body, for an hour, causes a rise of temperature of 1° C. ($1\frac{4}{5}$ deg. F.), and, if continued for another half hour, the temperature of the body rises 2° C. (Liebermeister). So, too, in the experiments of MM. Berger and Delaroche,** it was found that, after the body had been exposed to air of 120° during 17 minutes, a thermometer placed in the mouth rose nearly 7° above the ordinary temperature; it may be remarked, however, that as the body was immersed in a close box, from which the head projected (in order to avoid the direct influence of the heated air on the temperature of the mouth), the air had probably become charged with the vapour exhaled from the surface, and had therefore somewhat of the effects of a moist atmosphere. At any rate, the temperature of the healthy body does not appear to rise, under any circumstances, to a degree very much greater than this. In one of the experiments of Drs. Fordyce and Blagden,†† the temperature of a Dog, that had been shut up for half an hour in a chamber of which the temperature was between 220° and 236°, was found to have risen from 101° to about 108°. MM. Delaroche and Berger tried several experiments on different species of animals, in order to ascertain

* "Archiv für Anatomie u. Physiol.," 1860, pp. 520 and 589; 1861, p. 28; 1862, p. 661. "Archiv f. Klin. Medicin," Band v. p. 217.

† "Experiment. Beiträg. zur Kenntniss d. Wärmeregulirung Diss.," Dorpat, 1864.

‡ "Deutsch. Archiv f. Klin. Med.," Band iv. p. 323.

§ Virchow's "Archiv," Band xlv. p. 351; Band l. p. 354. ‖ "Physiologie," 1873, p. 308.

¶ Schuster, "Deutsche Klinik," 1864, pp. 216, 229, 248. Röhrig and Zuntz, Pflüger's "Archiv," Band iv. p. 57. Murri, "Del potere regulatore della temperatura animale." Pamphlet. Firenze, 1873. Rosenthal, "Centralblatt," 1872, p. 840.

** "Expériences sur les Effets qu'une forte Chaleur produit sur l'Economie," Paris, 1805; and "Journal de Physique," tomes lxiii. lxxi. et lxxvii.

†† "Philosophical Transactions," 1775.

the highest temperature to which the body could be raised without the destruction of life, by enclosing them in air heated from 122° to 201°, until they died: the result was very uniform, the temperature of the body at the end of the experiment only varying in the different species between 11° and 13° above their natural standard: whence it may be inferred that a sudden elevation to this degree must be fatal.* This elevation would be attained comparatively soon in a *moist* atmosphere; partly because of the greater conducting power of the medium, but principally on account of the check which is put upon the vaporization of the fluid secreted by the skin. Even here, however, custom and acquired constitution have a very striking influence; for whilst the inhabitants of this country are unable to sustain, during more than 10 or 12 minutes, immersion in a vapour-bath of the temperature of 110° or 120°, the Finnish peasantry remain for half an hour or more in a vapour-bath, whose temperature finally rises even to 158° or 167°. Death occurs in cold-blooded animals on sudden immersion in water at a temperature of from 98° to 102° F., in Mammals, for some minutes at a temperature of 109°—115° F., and in Birds of 120°—122° F. On examining the heart, it is found to have stopped, though it long continues to beat in ordinary asphyxia, and neither it nor any of the striated muscles respond to electrical or other stimuli, whilst cadaveric rigidity, due apparently to coagulation of the myosin, sets in with wonderful rapidity. The fatal effect of exposure to heat is attributed by Bernard† to the toxic influence of heat on striated muscular tissue, which speedily occasions the arrest of the cardiac and respiratory movements. The unstriated muscular fibres seem to be powerfully stimulated by these degrees of heat. The blood is dark and contains little oxygen (1 or 2 per cent.). The hand can with difficulty be borne in water at a temperature of 120° F.: higher temperatures produce acute pain. Pouchet‡ has endeavoured to show that, when small animals are exposed to cold, death results from changes occurring in the blood corpuscles; Walther§ has referred the fatal issue to anæmia of the nervous system. Both Dr. Davy‖ and Pouchet found that completely frozen animals were incapable of being restored to life.—Accurate experiments are yet wanting to determine the influence of humidity on the effects of *cold* air. From experiments on young Birds incapable of maintaining their own temperature, of which some were placed in cold dry air, and others in cold air charged with moisture, it was found by Dr. Edwards that the loss of heat was in both instances the same; the effect of the evaporation from the surface in the former case being counterbalanced in the latter by the depressing influence of the cold moisture. This influence, the existence of which is a matter of ordinary experience, is probably exerted directly upon the Nervous system.

388. Having thus considered the general facts which indicate the faculty possessed by the living system, in Man and the higher Animals, of keeping up its temperature to an elevated standard, and of preventing it from being raised much beyond it by any degree of external heat, we have next to inquire to what this faculty is due.¶—It may be stated as a general fact, that every

* Bernard ("Comptes Rendus de la Société de Biologie," 1859, p. 51) attributes the death of the animals in these and similar experiments to a condition analogous to rigor mortis of the heart being established. He found the auricles filled with blood, but the ventricles firmly contracted and empty.

† 'Leçons,' in the "Rev. Scientifique," 1871, p. 183. See also the same Review for 1876.

‡ "Journal de l'Anatomie," Jan. 1866. § "Centralblatt," April, 1866.

‖ "Proceed. of the Roy. Soc.," 1866, p. 250.

¶ It was affirmed by Dr. Granville ("Phil. Trans.," 1825) that the temperature of the uterus during parturition sometimes rises as high as 120°. In some observations made at

change in the condition of the organic components of the body, in which their elements enter into new combinations with Oxygen, *must* be a source of the development of Heat. And as we have seen that a considerable part of the carbonic acid and water which are exhaled in Respiration, is formed within the body by the metamorphosis of its own tissues, and that this metamorphosis is promoted by the active exercise of the nervo-muscular apparatus, it follows that in animals whose habits of life are peculiarly active, whilst the temperature of the surrounding medium is sufficiently high to prevent its exerting any considerable cooling influence over them, the combustive process thus maintained may be adequate for the maintenance of the temperature of the body at its normal standard. This seems to be the case with the great Carnivorous quadrupeds of warm climates, and with certain races of Men who lead a life of incessant activity like theirs. But whenever the cooling influence of the atmosphere is greater, or the retrograde metamorphosis of tissue takes place with less activity, some further supply of heat-producing material is required; and this is derived either directly from the food, or from a store previously laid up in the body. Although the albuminous and gelatinous components of the food may be made, by decomposition within the body, to yield saccharine and oleaginous compounds which serve as an immediate *pabulum* to the combustive process (§§ 80, 318), yet this metamorphosis involves a great waste of valuable nutritive material; and the needed supply is much more advantageously derived at once from those farinaceous or oleaginous substances, which are furnished in abundance by the Vegetable kingdom, the latter also by animals. No reasonable doubt can any longer be entertained, that the production of Heat by the combustive process is the purpose to which a large proportion of these substances is destined to be subservient in the bodies of Herbivorous animals and of Man; and the results of experience in regard to their relative heat-producing powers, are in precise accordance with the indications afforded by their chemical composition.

389. Our knowledge of the dependence of all the vital processes in warm-blooded animals upon the Heat of their bodies, and of the dependence of their calorifying power upon the due supply of material for the combustive process, has received some remarkable additions from the experiments of M. Chossat upon Starvation.* He found that Birds, when totally deprived of food and drink, suffered a progressive, though slight, daily diminution of temperature. This diminution was not so much shown by a fall of their maximum heat, as by an increase in the diurnal variation, which he ascertained to occur even in the normal state (§ 382, II.) The average variation in the *inanitiated* state was about 6° (instead of 1½°) gradually increasing as the animal became weaker; moreover, the gradual rise of temperature, which should have taken place between midnight and noon, was retarded; whilst the fall subsequently to noon commenced much earlier than in the healthy state; so that the *average* of the whole day was lowered by about 4½°, between the *first* and the *penultimate* days of this condition. On the *last* day, the production of heat diminished very rapidly, and the thermometer fell from hour to hour until death supervened: the whole loss on that day being about 25° Fahr., making the *total* depression about 29½°. This depression appears, from the considerations,

the Philadelphia Hospital, however, at the desire of Prof. Dunglison, the temperature of the uterus was not found to be much above that of the vagina; the former being, in three cases, 100°, 102°, and 106°, whilst the latter was 100°, 100°, and 105°. (Prof. Dunglison's "Human Physiology," 8th edit. vol. i. p. 602.)

* "Récherches Expérimentales sur l'Inanition," Paris, 1843; an analysis of this work will be found in the "Brit. and For. Med. Rev.," April, 1844. See also H. Senator, in Reichert and Du Bois-Reymond's "Archiv," 1872, p. 1.

to be presently stated, to be the *immediate* cause of Death.—On examining the amount of loss sustained by the different organs of the body, it was found that 93 per cent. of the *Fat* had disappeared; being all, in fact, which *could* be removed; whilst the nervous centres scarcely exhibited any diminution in weight (§ 80). From the constant coincidence between the entire consumption of the fat, and the depression of temperature, joined to the fact that the duration of life under the inanitiating process evidently varied (other things being equal) with the amount of fat previously accumulated in the body, the inference seems irresistible, that the calorifying process depended chiefly on the materials supplied by this substance. Whenever, therefore, the store of combustible matter in the system was exhausted, the inanitiated animals died, by the cooling of their bodies consequent upon the loss of calorifying power.

390. That this is the real explanation of the fact was shown by the results of a series of very remarkable experiments performed by M. Chossat, with the purpose of testing the correctness of this view. When inanitiated animals whose death seemed impending (death having actually taken place in several instances whilst the preliminary processes of weighing, the application of the thermometer, &c., were being performed), were subjected to artificial heat, they were almost uniformly restored from a state of insensibility and want of muscular power to a condition of comparative activity; their temperature rose, their muscular power returned, they flew about the room, and took food when it was presented to them; and if the artificial assistance was sufficiently prolonged, and they were not again subjected to the starving process, most of them recovered. If they were left to themselves too early, however, the digestive process was not performed, and they ultimately died. Up to the time when they began to take food, their weight continued to diminish; the secretions being renewed, under the influence of artificial heat, sometimes to a considerable amount. It was not until digestion had actually taken place (which, owing to the weakened functional power, was commonly many hours subsequently to the ingestion of the food), that the animal regained any power of generating heat; so that, if the external source of heat was withdrawn, the body at once cooled; and it was not until the quantity of food actually *digested* was sufficient to support the wants of the body, that its independent power of calorification returned. It is to be remembered that, in such cases, the resources of the body are on the point of being completely exhausted, when the attempt at re-animation is made; consequently, it has nothing whatever to fall back upon; and the leaving it to itself *at any time* until fresh resources have been provided for it, is consequently as certain a cause of death as it would have been in the first instance.

391. It can scarcely be questioned, from the similarity of the phenomena, that Inanition, with its consequent depression of temperature, is the immediate cause of death in various Diseases of Exhaustion: and it seems probable that there are many cases in which the depressing cause is of a temporary nature, and in which a judicious and timely application of artificial heat might prolong life until it has passed off, just as artificial respiration is serviceable in cases of narcotic poisoning. It is especially, perhaps, in those forms of Fever, in which no decided lesion can be discovered after death, that this view has the strongest claim to reception; and the beneficial result of the administration of Alcohol in such conditions, and the large amount in which it may be given with impunity, may probably be accounted for on this principle. That it acts as a specific stimulus to the Nervous system, cannot be doubted from its effects on the healthy body; but that it serves as a *fuel* to

keep up the calorifying process, appears equally certain.* Its great efficacy in such cases seems to depend upon the readiness with which it will be taken into the circulation, by a simple act of endosmotic imbibition, when the special Absorbent process, dependent upon the peculiar powers of the cells of the villi (§ 139), is in abeyance. There is no other combustible fluid, whose miscibility and whose density, relatively to that of the Blood, will permit of its rapid absorption by the simple physical process adverted-to.†

392. That the oxidation of certain components of the tissues is the fundamental source of Animal Heat, is further indicated by the close conformity which we everywhere find, between the activity of the Respiratory process and the amount of Heat which is generated; and this not merely when we compare different tribes of animals with each other, but also when we compare the amount of oxygen absorbed and of carbonic acid exhaled by the same individuals under different degrees of external temperature (§ 287, I.) For we find that the system possesses within itself a regulating power, by which the combustive process is augmented in activity when the cooling influence of the surrounding medium is considerable, so that this influence is resisted; whilst the internal fire (so to speak) is slackened, whenever the temperature of the outer air rises so much as to render the same generation of heat no longer requisite. The appetite for food, and especially for those particular forms of it which best afford the combustive pabulum, varies in the same degree; and thus, when supplied with appropriate nutriment, Man is able to brave the severest cold, without suffering any considerable depression in his bodily temperature.—It would seem that the Cutaneous Respiration (§ 289), small as its amount is, promotes those molecular changes on which the maintenance of Animal Heat depends; for it was found by MM. Becquerel and Breschet,‡ and Socoloff,§ that when the hair of Rabbits was shaved off, and a composition of glue, suet, and resin (forming a coating impermeable to the air) was applied to the whole surface, the temperature rapidly fell, notwithstanding the obstacle thus offered to the evaporation of the sweat, whereby, it might be supposed, the temperature of the body would be considerably elevated. In the first rabbit, which had a temperature of 100° before being shaved and plastered, it had fallen to 89½° by the time the material spread over him was dry. An hour afterwards, the thermometer placed in the same parts (the muscles of the thigh and chest) had descended to 76°. In another rabbit, prepared with more care, by the time that the plaster was dry, the temperature of the body was not more than 5½° above that of the surrounding medium, which was at that time 69½°; and in an hour after this the animal died. The varnish appears to act by increasing radiation. Dr. Sanderson‖ found that a rabbit, which in the normal state gave off only 3 heat-units in ten minutes, gave about 20 after varnishing, notwithstanding that in the former case its temperature was constant at 39·5° C., while in the other it sank from 36° to 25°. In Socoloff's experiments, albumin rapidly made its appearance in the urine, and tetanic convulsions occurred before death. Neither wrapping the animal in wool, nor compelling it to breathe oxygen, prevented the fatal result. After death a diffused parenchymatous inflammation of the kidneys was observed, and ulcers were

* See the articles written by M. Baudot in "L'Union Médicale" for Nov. 1863.

† The Author has stated the very striking results of observations which he has had the opportunity of making upon this point, in his Essay on the "Physiology of Temperance and Total Abstinence."

‡ "Comptes Rendus," October, 1841. These experiments were repeated and confirmed by Magendie ("Gazette Médicale," Dec. 6th, 1843).

§ "Centralblatt," 1872, No. 44. ‖ "Handbook for the Physiol. Labor.," 1873, p. 333.

found in the stomach consequent upon profound extravasation. These experiments and observations, though not strictly applicable to man,* place in a very striking point of view the importance of the cutaneous surface as a respiratory organ, even in the higher animals; and they enable us to understand how, when the aërating power of the Lungs is nearly destroyed by disease, the heat of the body is kept up to its natural standard by the action of the skin. A valuable therapeutic indication, also, is derivable from the knowledge which we thus gain, of the importance of the cutaneous respiration; for it leads us to perceive the desirableness of keeping the skin moist, in those febrile diseases in which there is great heat and dryness of the surface, since aëration cannot properly take place through a dry membrane. Of the relief afforded by cold or tepid sponging in such cases experience has given ample evidence.

393. It has been held that the Chemical theory of Calorification is insufficient to account for the total amount of Heat generated by a warm-blooded animal in a given time; this assertion being founded upon the experimental results obtained by M. Dulong. MM. Favre and Silbermann† have shown, however, that the original estimates require correction for the true calorific equivalents of carbon and hydrogen; and that this correction having been made, the heat produced by the combustion of the Carbon which is contained in the carbonic acid expired, and by the combustion of such a proportion of the Hydrogen contained in the exhaled water as may be fairly considered to have undergone oxygenation within the system (§ 294), proves to be adequate to compensate for that which would be dissipated by the evaporation of all the water transpired from the skin and lungs, and also to maintain the temperature of the body itself in an atmosphere of ordinary coolness. And to the combustion heat of carbon and hydrogen we should also add that of those relatively minute quantities of Phosphorus and Sulphur, which also undergo oxidation within the system (§ 366), whereby a small additional amount of heat must be generated.—Through whatever diversity of combinations or successive stages of oxidation these elements respectively pass, in their progress to complete or final oxidation, it may be regarded as an indisputable fact, that *they give out precisely the same amount of heat in the whole, as if they had undergone the most rapid combustion to the same degree of oxidation in pure oxygen;* and thus almost every molecular change in the body, but pre-eminently those which are concerned in the *disintegration* of its textures, and in the elimination of their products by Respiration, participate in the function of Calorification.—The experiments of Ranke,‡ made upon himself, furnish perhaps the best data on which the absolute amount of heat developed in the body can be calculated; and they are by so much the more to be depended upon, as the results agree well with the determinations of Frankland on the amount of heat developed by various kinds of aliment during the act of combustion. It may be remarked that the age of Ranke was twenty-four, his height about six feet, and his weight 154 lbs. The first experiment was made to determine the amount of heat developed on mixed food. The ingesta and the egesta were equal in amount, the weight of the body remaining the same. The numbers represent grammes:—

Exp. 1.—*Production of heat on the first day of total abstinence* from food (commencing 23 hours after the last meal), the ingesta (*i.e.*, consumption of the body itself) calculated from the egesta:—

* Senator, Virchow's "Archiv," Band lxx. Heft ii. p. 12.

† See their Memoirs 'Des Chaleurs de Combustion,' in "Comptes Rendus," tom. xx. xxii.

‡ "Grundzüge der Physiologie," 1874, p. 566.

Ingesta in Grammes.	Egesta.
54·45 Albumin	18·3 Urea.
195·94 Fat	0·24 Uric Acid.

From these data it may be calculated that the daily production of heat amounted to 2012·8 calories.

Exp. II.—*Production of heat on meat diet*, the decomposition of flesh in the body, and the consumption of fat being calculated from the excretions:—

Ingesta.	Egesta.
1832 grm. of Meat, of which only 1300 grm. underwent disintegration.	86 Urea.
70 grm. Fat of Food / 75·14 Fat of Body \ 145·14 Fat.	1·95 Uric Acid.
	99 Fæces.

The daily production of heat produced here was 2799·5 calories.

Exp. III.—*Production of heat on non-nitrogenous diet*, consumption of albumin and deposit of fat in the body calculated from the excreta:—

Ingesta in grammes.	Egesta.
51·55 Body Albumin.	17·1 Urea.
150·00 Fat, of which 81·5 were deposited. So that only 68·5 were burnt off.	0·54 Uric Acid.
	90·0 Fæces.
300 Starch.	
100 Sugar.	

The daily production of heat was here 2059·5 calories. With mixed diet the daily production was about 2200 calories.

Thus during Fasting . . .	2012	Calories	were produced per diem.
On Non-Nitrogenous Diet . .	2059	„	„ „
On Mixed Diet	2200	„	„ „
On abundant Meat Diet . .	2779	„	„ „

According to Senator,* a dog weighing about 12 lbs., fed on a pound of meat per diem, gave off, 16-26 hours after food, 12-14 calories per hour, during which time it excreted from 52 to 57 grains of carbonic acid gas. After fasting for 48 hours, it gave off 11·6 calories, and eliminated 51·7 grains of CO_2, whilst two hours after digestion it gave off 21 calories, and eliminated 79·8 grains of CO_2.

The average of Ranke's experiments on himself gave the number of calories produced per diem at 2200, which is a quantity sufficient to raise 44 pounds of water from the freezing to the boiling point. Helmholtz estimated the amount at 2700.† The mode in which the heat produced is applied, has been estimated as follows—

To the elevation to the temperature of the body of the food ingested	70	Calories	2·6 per cent.
To the warming of the air breathed (air at 32° F.)	140	„	5·2 „
Or if the air be at 68° F.	70	„	2·6 „
To the vaporization of the water discharged by the lungs . . .	397	„	14·7 „
To the radiation from the body and evaporation from the skin .	2195	„	77·5 „

In this calculation Helmholtz estimated that one kilogramme of water (= 2·2 lbs. avoird.) in evaporating from the skin and lungs took up or required 582

* "Centralblatt," 1871, p. 738.

† Or rather 2,700,000, but he considered a calory to be the quantity of heat required to raise 1 gramme of water 1° C., instead of 1 kilogramme, which is 1000 grammes. The mechanical equivalent of heat recently given by Mr. J. P. Joule ("Proceed. Roy. Soc. 1878," vol. xxvii. p. 38) is that, taking a unit of heat, *i.e*, the heat required to raise 1 lb. of water weighed in vacuo from 60° to 61° F., its mechanical equivalent reduced to the sea level is 772·55 foot pounds.

calories, its temperature being already nearly 100° F. Food was considered to be upon the average about 20° F. cooler than the temperature of the body, and to require the same amount of heat to warm it as water. Barral* gives a somewhat different estimate, and considers that of the total heat produced in a man at rest, which, in accordance with Helmholtz, he estimates at 2706·076 calories, 699·801, or 25·85 per cent., are lost in the water evaporated from the skin and lungs; 100·811, or 3·72 per cent., in warming the air breathed; 52·492, or 1·94 per cent., in warming the food; 33·020, or 1·22 per cent., in the solid and fluid excreta; and 1819·952, or 67·22 per cent., by radiation and conduction and mechanical work. Béclard† estimates that a man daily developes sufficient heat to raise 55 lbs. of water from 32° to 212° F.

394. *Local Variations.*—The blood is the means by which the uniformity of the temperature of the body generally is maintained, and its mass enables it to equalize the variable amounts that are produced in the several glands and muscles it traverses, according to whether they are in an active or in a quiescent condition. Warmed during its passage through the abdominal and thoracic viscera, which are in constant functional activity, and which are prevented from cooling by the thick layer of fat that covers the abdominal parietes, the blood carries a high temperature to the extremities, where it becomes gradually reduced, owing to radiation and conduction. If the heat be prevented from escaping from the surface of the body by radiation or evaporation, as in cases where the large size of the animal causes the capillaries of the skin to bear a comparatively small proportion to those of the body generally, or when the animal possesses a thick coating of wool or fat, or is kept in a warm atmosphere, the temperature rises to a high degree: when the opposite conditions are present, the temperature readily falls. Eulenburg and Landois‡ found that stimulation of the cervical sympathetic in rabbits caused cooling of the ear, which lasted from 15—20 secs. after the removal of the stimulation, and was followed by exaltation above the original temperature. Section of the cervical sympathetic caused cooling in the first instance, lasting for ten secs., and amounting to $\frac{1}{10}$ to $\frac{1}{5}$° C., which was followed by a rapid rise of several degrees, whilst stimulation of the peripheral stump immediately caused a fall. Section of the sciatic in a slightly curarized dog caused a rise of 2—3° C. in the corresponding foot, whilst irritation of the peripheral stump caused a fall after a latent period of 15 secs. After a time it sank no further, but slowly rose again. On second stimulation it fell, but after a longer latent stage and to a less degree. The importance of the active circulation of the blood through the vessels of a part in maintaining its temperature is shown by the fact that if the arterial current in the arm be obstructed by compressing the brachial artery, or if the brachial vein be tied, the temperature in the closed hand falls 2° C. (3—6° F.) below that of the opposite one.§ It was also well shown in the experiments of Claude Bernard,‖ that an elevation of temperature constantly took place on one side of the face, when the trunk which unites the Sympathetic ganglia of the neck on that side was cut through; this increase being not only perceptible to the touch, but showing itself by a thermometer introduced into the nostrils or ears, even to the extent of from 7° to 11° Fahr. When the superior cervical ganglion was removed, the same effect was produced, and with yet greater intensity. This difference is main-

* "Stat. Chim. des Animaux," Paris, 1850. † "Physiol.," 1862, p. 561.
‡ Virchow's "Archiv," Band lxvi. Heft 4, and Band lxviii. Heft 2.
§ Adæ, "Centralblatt f. d. Med. Wiss.," 1877, p. 86.
‖ "Gazette Médicale," Févr. 21, 1852.

tained for many months, and is not apparently connected with the occurrence of inflammation, congestion, œdema, or any other pathological change in the tissues, though the sensibility of the parts thus affected is no less augmented than their temperature; moreover, it is not prevented from manifesting itself by the division of any of the cerebro-spinal nerves of the face. This exaltation of temperature, there can be no doubt, is sufficiently explained by the relaxation of the walls of the smaller arteries (producing a state resembling a permanent "blush"), and the consequent increase in the flow of blood through the part, which has been shown by Dr. Aug. Waller to result from this operation. (See § 238.) A curious experiment made by Bernard tends to show that the quantity of blood taken up by any one organ is supplied to it at the expense of another; and that the excess of heat developed at one point of the body is compensated for by a diminution in some other part. He found that on making a section of the Sympathetic in the neck of a Rabbit, both of whose ears had previously a temperature of 95° F., the temperature rose to 100° F. on the side on which the section was made, whilst it fell to 91° F. on the opposite side. When, however, the peripheral end of the cut nerve was galvanized, the temperature fell in the corresponding ear, and rose in the opposite one.* Local variations of temperature occur in the various organs in consonance with the changes in the circulation in them resulting from the active performance of their duties, or their state of repose. In some instances, however, such variations seem to be independent of changes in the supply of blood.† Thus Schiff‡ has shown that irritation of a sensory nerve in a dog under the influence of curare, and therefore incapable of performing muscular movements, causes increase of the temperature of one or the other hemispheres of the brain, and was independent of changes in the circulation, since it occurred even as late as twelve minutes after the heart's action had ceased. Even irritation of the nerves of special sense will produce this effect, for it was distinctly perceptible in a thoroughly curarized dog before which an umbrella was suddenly opened. In accordance with this, though perhaps other circumstances lead to the increase of temperature, is the observation made by Bernard,§ that if the foot of a dormouse be pinched whilst in a state of hybernation, the temperature rises almost immediately as much as from 60° to 70° F. In opposition to it is the statement made by Horvath,‖ that irritation of a sensory nerve causes depression of the temperature in the rectum.¶ Horvath having observed that mere binding of a rabbit so that it could not move caused a gradual fall of temperature, sometimes to as much as 3° Fahr., at first attributed it to its cramped condition; but further experiments led him to conclude that it was due to the pain experienced by the animal when its limbs were tightly bound. Funke** states that intellectual exertion causes an increase of temperature in the brain. A considerable fall of temperature occurs during the narcotic condition induced by chloroform,†† which is probably partly due to its depressing influence upon the circulation, as well as to its direct action upon the blood corpuscles. In like manner in poisoning by curare, which C. Bernard has shown first paralyses the vaso-motor nerves, causing dilatation of the cutaneous capillaries, and consequent increased loss of heat, and at the

* Bernard, "Leçons," 1859, 6me Leçon.

† Many instances of local variations in disease have been collected by Wunderlich.

‡ "Archives de Physiologie," 1870, p. 198. § "Rev. Scient.," 1871, p. 288.

‖ "Centralblatt," 1870, p. 546. ¶ See also Heidenhain, "Centralblatt," 1869.

** "Physiologie," 1873, p. 306. See also Lombard, "Proceed. Roy. Soc.," vol. xxvii. 1878, p. 166.

†† See Scheinesson, "Dissert. über d. Einfluss d. Chloroform:" quoted by O. Funke, "Physiologie," 1872, p. 308.

same time a retardation of the movements of the heart and respiratory muscles, a decline of temperature is constantly observed. Jacobson and Landré* have shown that there is similarly a decline in the temperature of the rectum.

395. We have now to inquire whether the *power of generating Heat* is possessed by the Human subject in an equal degree at all ages; this question being very different from that of the *ordinary temperature* of the body at the various periods of life; since an individual who can maintain a high temperature when the surrounding air is moderately warm, may have very little power of bearing continued exposure to severe cold. Important analogical evidence on this point has been supplied by the experiments of Dr. W. F. Edwards upon the lower Mammalia, Birds, &c.† It appears from these to be a general fact, that, the younger the animal, the less is its independent calorifying power. Thus the development of the embryo of all Oviparous animals is entirely dependent upon the amount of external warmth supplied to it. There are many kinds of Birds, which, at the time they issue from the egg, are so deficient in the power of generating heat, that their temperature rapidly falls when they are removed from the nest and placed in a cold atmosphere; it being shown by collateral experiments, that the loss of heat was not to be attributed to the absence of feathers, nor to the extent of surface exposed in comparison with the bulk of the body; and that nothing but an absolute deficiency in the power of generating it, would account for the fall of temperature. This is quite conformable to facts well ascertained in regard to Mammalia. The fœtus, during intra-uterine life, has little power of keeping-up its own temperature; and in many cases it is much dependent on external warmth for some time after birth. The degree of this dependence, however, differs greatly in the various species of Mammalia, as among Birds; being less, in proportion as the general development is advanced. Thus, young Guinea-pigs, which can run about and pick up food for themselves almost as soon as they are born, are from the first independent of parental warmth; whilst, on the other hand, the young of Dogs, Cats, Rabbits, &c., which are born blind, and which do not for a fortnight or more acquire the same development with the preceding, rapidly lose their heat when withdrawn from contact with the body of the mother.

396. In the Human species, it is well known that external warmth is necessary for the Infant, its body rapidly losing heat when exposed to the chilling influence of a low temperature; but the fact is too often neglected (under the erroneous idea of 'hardening' the constitution) during the early years of childhood. It is to be carefully remembered, that the development of Man is slower than that of any other animal, and that his calorifying power is closely connected with his general bodily vigour; and though the infant becomes more independent of it as development advances, it is many years before the standard can be maintained without assistance, throughout the ordinary vicissitudes of external temperature. Especial care is required with regard to the maintenance of the bodily heat by artificial warmth, in the case of children prematurely born; for the earlier the period of embryonic life, the less is the power of calorification that exists for some time after birth. The temperature of a seven months' child, though well swathed and near a good fire, was found by Dr. W. Edwards, within two or three hours after its birth, to be no more than 89·6°. And in some of the recorded instances in which the birth has taken place before the completion of the sixth month, it has not

* "Nederland. Archiv v. Genees en Naturk.," Band ii. p. 355.

† "On the Influence of Physical Agents on Life," part iii. chap. i.

been found possible to maintain the warmth of the infant by exposure to the radiant heat of a fire, the contact of the warm body of another person being the only effectual means of keeping up its temperature.—The fullest measure of calorifying power is possessed by adults; but even in them it is sometimes weakened by previous exertion, so that death by the cooling of the body may occur, when the body is exposed to cold of no great intensity, but in a state of exhaustion of nervous power; a fact which remarkably confirms the views advanced in the preceding paragraph (§ 395). A decrease of calorifying power takes place in advanced age. Old people complain that their "blood is chill;" and they suffer greatly from exposure to cold, the temperature of the whole body being lowered by it.

397. These facts have a very interesting connection with the results of statistical inquiries, as to the average number of deaths at different seasons; the following are recorded by M. Quetelet,* as occurring at Brussels, the *mean* monthly mortality at each age being reckoned as 100.

——	First Month.	2—3 Years.	8—12 Years.	25—30 Years.	50—65 Years.	90 Years and above.
January	1·39	1·22	1·08	1·05	1·0	1·58
February	1·28	1·13	1·06	1·04	1·22	1·48
March	1·21	1·30	1·27	1·11	1·11	1·25
April	1·02	1·27	1·34	1·06	1·02	0·96
May.	0·93	1·12	1·21	1·02	0·93	0·84
June	0·83	0·94	0·99	1·02	0·85	0·75
July	0·78	0·82	0·88	0·91	0·77	0·64
August.	0·79	0·73	0·82	0·96	0·85	0·66
September. . . .	0·86	0·76	0·81	0·95	0·89	0·76
October	0·91	0·78	0·76	0·93	0·90	0·74
November	0·93	0·91	0·80	0·97	1·00	1·03
December	1·07	1·01	0·96	0·97	1·15	1·29

We see from this table that, during the first months of infant life, the external temperature has a very marked influence; for the average mortality during each of the three summer months being 80, that of January is nearly 140, and the average of February and March is 125. This is confirmed by the results obtained by MM. Villermé and Milne-Edwards, in their researches on the mortality of the children conveyed to the Foundling Hospitals in the different towns in France; for they not only ascertained that the mortality is much the greatest during the first three months in the year, but also that it varies in different parts of the kingdom, according to the relative severity of the winter.† As childhood advances, however, the winter mortality diminishes, whilst that of the spring undergoes an increase; this is probably due to the greater prevalence of epidemics at the latter season; for the same condition is observed, in a still more remarkable degree, between the ages of 8 and 12 years,—the time when children are most severely affected by such epidemics. As the constitution acquires greater vigour, and the bodily structure attains its full development, the influence of the season upon

* "Essai de Physique Sociale," tom. i. p. 197.

† Dr. Emerson has shown that, in the Southern and Middle States of North America, the *high summer* temperature is the greatest cause of Infant-mortality: the proportion of deaths during the first year of childhood occurring in the months of June, July, and August, being about *four* times greater than that occurring during the same months in any subsequent year up to the age of 20. The *winter* mortality under the second year scarcely exceeds the average of subsequent years. ("Amer. Jour. of Med. Sci." Nov. 1831.)

mortality becomes less apparent; so that at the age of from 25 to 30 years, the difference between the summer and winter mortality is very slight. The difference reappears, however, in a very marked degree, at a later period, when the general vigour, and the calorifying power, undergo a gradual diminution. Between the ages of 50 and 65, it is nearly as great as in early infancy; and it gradually becomes more striking, until, at the age of 90 and upwards, the deaths in January are 158 for every 74 in July (a proportion of $2\frac{1}{2}$ to 1); and the average of the three winter months is 145, whilst that of the three summer months is only 68, or less than one-half.—The results of the comparisons which have now been carried out for many successive years in the Reports of the Registrar-General, between the variations in the weekly rate of mortality in the Metropolis and the range of atmospheric temperature, present a close coincidence with the foregoing: it being especially to be noted, that the rate of mortality (save during the prevalence of any fatal epidemic) is almost invariably the highest during the winter months; that the increase of deaths at that period is most marked amongst children and old people; and that any extraordinary severity of winter cold constantly produces a great augmentation in the mortality, the weekly number of deaths rising from the average of 1100 (or thereabouts) to 1600 or even 1800, when the mean temperature of the week remains six or eight degrees below the freezing point.

3. *Evolution of Light.*

398. Although the evolution of Light from the living Human subject is an exceptional phenomenon, which has only been observed in morbid states of the body, yet its occasional occurrence is fraught with interest to the Physiologist, on the one hand, from its relation to the Luminosity so common among the lower animals, and on the other from the indications which it affords of the possibility of the formation, even during life, of peculiar phosphuretted compounds, which, being products of incipient decomposition, have been usually supposed to be generated only after death.—There is no doubt that luminous exhalations frequently ascend from burial-grounds; and that the superstitions of many nations respecting "corpse-lights" have to this extent a foundation in fact. A very decided luminosity has been observed to proceed from dissecting-room subjects, the light thus evolved being sufficient to render the forms of the bodies, as well as those of muscles and other dissected parts (which are peculiarly bright), almost as distinct as in the daylight. That this proceeds from the production of a peculiar phosphorescent compound, is shown by the fact, that the luminosity may be communicated to the fingers or to towels, &c., by contact with the luminous surfaces.*—Dr. W. Stokes narrates the case of a patient who was under his observation, some years since, in the Old Meath Hospital, having been admitted on account of an enormous cancer in her breast, which was in an advanced stage of ulceration, the edges being irregular and everted; every part of the base and edges of this cavity was strongly phosphorescent, the light being sufficient to enable the figures on a watch-dial to be distinguished within a few inches; and here also it appeared that the luminosity was due to a particular exudation from the exposed surface. Three cases are recorded by Sir H. Marsh, in which an evolution of light took place from the living body, without any such obvious source of decomposition; all the subjects of these cases, however, were in the last stage

* See Sir Herbert Marsh on "The Evolution of Light from the Living Human Subject" (Dublin, 1842), p. 20.—From this interesting pamphlet most of the statements in this paragraph are derived. See also Herbert Spencer, "Principles of Biology," vol. i. p. 46.

of phthisis; and it can scarcely be doubted that here, as in other diseases of exhaustion, incipient disintegration was taking place during the latter periods of life (§ 82). The light in each case is described as playing around the face, but not as directly proceeding from the surface; and in one of these instances, which was recorded by Dr. D. Donovan,* not only was the luminous appearance perceptible over the head of the patient's bed, but luminous vapours passed in streams through the apartment. It can scarcely be doubted that it was here the *breath* which contained the luminous compound, more especially as it was observed in one of the cases to have a very peculiar smell; and the probability that the luminosity was due to the presence of phosphorus in progress of slow oxidation, is greatly increased by the fact already referred to (§ 295), that the injection of phosphuretted oil into the blood-vessels gives rise to a similar appearance. In repeating this experiment, Sir H. Marsh states that when half an ounce of olive-oil, holding two grains of phosphorus in solution, was injected into the crural vein of a dog, a dense white vapour began to issue from the nostrils even before the syringe was completely emptied, which became faintly luminous on the removal of the lights: and the injection being repeated with the same quantity, the expiration immediately became beautifully luminous, resembling jets of pale-coloured flame pouring forth from the nostrils of the animal. And the luminosity which has been occasionally observed in the urine† may fairly be imputed to an increase in the quantity of unoxidized phosphorus which it seems normally to contain; its liberation taking place at a more rapid rate than its conversion into phosphoric acid, either through excessive excretion or through impeded respiration.‡ A case has been recorded by Kaster in which the body linen was rendered luminous by the perspiration after any violent exercise; and here, too, the cause may be presumed to have been the same.—On the whole, then, we may conclude the occasional evolution of Light from the Human subject, to be the consequence (when not an *electrical* phenomenon) of the production of a phosphorescent compound at the expense of the disintegrating tissues; which compound passes off through one of the ordinary channels of excretion.

4. *Evolution of Electricity.*

399. When the vast variety of changes of condition to which the components of the living body are subjected during the performance of its vital operations, and the impossibility of the occurrence of any of these without some disturbance of Electric equilibrium,§ are duly considered, the wonder

* "Dublin Medical Press," Jan. 15, 1840.

† Casper's "Wochenschrift," 1849, No. 15.—A case has been put on record (Büchner's "Repert., Band viii. p. 342) in which the urine and semen of a patient who was under treatment for impotence and spermatorrhœa, and who was employing phosphorus as a remedy both internally and externally, were observed to be luminous.

‡ The large proportion of intemperate subjects, among those who exhibit this phenomenon, seems to confirm the view already expressed, that the habitual presence of Alcohol in the blood interferes with the oxidation and elimination of excrementitious matters.

§ There is probably no instance of *chemical union* or decomposition, in which the electric condition of the bodies concerned is not altered. Simple *change of form*, from solid to liquid, or from liquid to gaseous, is attended with electric disturbance; and this is greatly increased when any separation takes place between substances that were previously united, as when water containing a small quantity of saline matter is caused to evaporate and to leave it behind. *Heat*, again, is continually generating Electricity; for not only is a current produced by the heating of two dissimilar metals in contact, but also by the unequal heating of two parts of the same bar; and though the effect is most striking in the case of metals, it is by no means limited to them. And so constantly is Electricity generated by the retardation

is, not that such disturbance should be occasionally so considerable as to make itself apparent, but that it should be ordinarily so obscure as only to be detected by the most careful search, and with the assistance of the most delicate instruments. The researches of Prof. Matteucci, M. du Bois-Reymond, and others, however, have now made it apparent that there are no two parts of the body (save those which correspond on the opposite sides), whose electrical condition is precisely the same; and that the differences between them are greater in proportion to the diversity of the vital processes which are taking place in them, and to the activity with which these are being carried on.*— It is by the comparison of the electric states of different secreting surfaces, that such departures from equilibrium are most readily demonstrated. Thus, Donné found that the skin and most of the internal membranes are in opposite electrical states; and Matteucci observed a considerable deflection of the needle of a delicate galvanometer, when the liver and stomach of a rabbit were connected with its platinum electrodes.† More recently, Mr. Baxter has found that if one of the electrodes be placed upon any part of the intestinal surface, and the other be inserted into the branch of the mesenteric vein proceeding from it, a decided deflection of the needle is produced, indicating a positive condition of the blood; but that no effect is produced when the second electrode is inserted into the artery of the part, instead of into its vein. These effects were found to cease after the death of the animals; and could not be attributed, therefore, to mere chemical differences between the blood and the secreted product; but must have arisen from electric disturbance taking-place in the very act of secretion.‡ Scoutetten and Shettle,§ again, have found arterial blood to be positive in its relations to venous blood.— That the process of Nutrition, as well as of Secretion, in parts which are undergoing rapid molecular change, gives rise to electric disturbance, is proved by the experiments of Matteucci and du Bois-Reymond, upon the relative electrical states of different parts of muscles and nerves. If the two extremities of a Muscle, removed from the body of an animal very recently killed, be applied to the two electrodes of a delicate galvanometer, there is usually some deflection of the needle; this being greater, in proportion to the difference in the arrangement of the muscular and tendinous elements at the two extremities. Although the direction of the current is constant for each muscle, yet there is no constant relation between the direction of the currents and the position of the muscles in the body; thus in the *gastrocnemius* of the Frog's leg, the direction is from the foot towards the body, whilst in the *sartorius* it is the reverse. Taking all the muscles of a part together, however, there is usually such a want of balance between the opposite currents,

of *motion*, as in friction, that it is not possible to rub together any two substances, excepting those which are of the most perfect homogeneity (such as the fractured surfaces of a broken bar), without the production of Electric change as well as of Heat.

* Having had an opportunity of witnessing some of the experiments made by M. du Bois-Reymond with a magneto-electrometer of extraordinary sensitiveness, the Author can bear his personal testimony to the fact, that the electricity even of the corresponding fingers of the two hands is very seldom equally balanced, and that the existence of even the slightest scratch or abrasion of surface upon one of them produces a very marked disturbance.

† See M. Becquerel's "Traité de l'Electricité," tom. i. p. 327, and tom. iv. p. 300. From his researches on the electrical organs of the Torpedo, Prof. Babuchin ("Centralblatt," 1870, p. 241) arrives at the conclusion that they are essentially muscles in which the proper muscular or contractile substance is absent, and conversely he regards muscles as electrical organs, in which muscular fibres are introduced between the electrical septa. Marey estimated ("Comptes Rendus," lxxiii. p. 918 and 958) the period of latent excitation of the electrical apparatus of the torpedo to be 1–60th of a second, whilst that of the muscles of the frog is 1–80th.

‡ "Philosophical Transactions," 1848, p. 243.

§ "An Essay on the Electricity of the Blood," 1867.

that a constant current is established in the direction of the strongest and most numerous of the separate muscular currents; this, in the Frog, passes uniformly from the hind-feet towards the head, and was at one time supposed to be peculiar to that animal; but a similar current may almost always be detected in other animals. The muscular current grows feebler and feebler, the longer the muscle has been removed from the body; it is affected by any agents which tend to lower its vitality, and becomes extinct as soon as its contractility ceases. From the experiments of M. du Bois-Reymond, it may be concluded that the current in the arm of Man, when at rest, is from the shoulder towards the points of the fingers. (The special conditions of the 'Nervous' and 'Muscular' currents will be hereafter fully considered in the chapters devoted to the Nerves and Muscles respectively.)

400. Some of the most important parts of the body being thus in a state of constant *disequilibrium* with regard to each other, it is not surprising that the Electric state of the whole should be ordinarily in disequilibrium with that of surrounding bodies. This difference, however, is usually prevented from manifesting itself, in consequence of the restoration of the equilibrium by the free contact which is continually taking place between them; and it is for the most part only when the Human body is insulated, that it becomes apparent. The galvanometer is then affected, however, by the contact of one of its electrodes with the person insulated, and the other with any neighbouring uninsulated body; and also by the contact of the electrodes with the hands of two persons both insulated, who join their other hands together, a difference in the electrical states of the two individuals being thus indicated. The electricity of Man is most commonly positive, and irritable men of sanguine temperament have more free electricity than those of phlegmatic character. The electricity of women is more frequently negative than that of men. There are persons who scarcely ever pull off articles of dress which have been worn next the skin, without sparks and a crackling noise being produced; especially in dry weather, when the electricity of the body is retained, instead of being rapidly dissipated as it is by a damp atmosphere. The effect is usually heightened, if silk stockings and other silken articles have been worn, since these act as insulators. It is doubtless in part attributable to the friction of the articles of dress against each other and against the body; but we can scarcely doubt that it is partly due to the generation of electricity in the body itself, since it bears no constant relation to the former of these supposed causes. Thus a Capuchin friar is mentioned by Dr. Schneider,* who, on removing his cowl, always found a number of shining crackling sparks to pass from his scalp; and this phenomenon continued still perceptible after a three weeks' illness.—The most remarkable case of the generation of Electricity in the Human subject at present known, was recorded some years since in America.† The subject of it, a lady, was for many months in an electric state so different from that of surrounding bodies, that whenever she was but slightly insulated by a carpet or other feebly conducting medium, sparks passed between her person and any object she approached; when most favourably circumstanced, four sparks per minute would pass from her finger to the brass ball of the stove at the distance of $1\frac{1}{2}$ inch. From the pain which accompanied the passage of the sparks, her condition was a source of much discomfort to her. The circumstances which appeared most favourable to the generation of the electricity, were an atmosphere of about 80°, tranquillity of mind, and social enjoyment; whilst a low

* Casper's "Wochenschrift," 1849, No. 15.

† "American Journal of Medical Sciences," January, 1838.

temperature and depressing emotions diminished it in a corresponding degree. The phenomenon was first noticed during the occurrence of an Aurora Borealis; and though its first appearance was sudden, its departure was gradual. Various experiments were made, with a view of ascertaining if the electricity was generated by the friction of articles of dress; but no change in these seemed to modify its intensity.

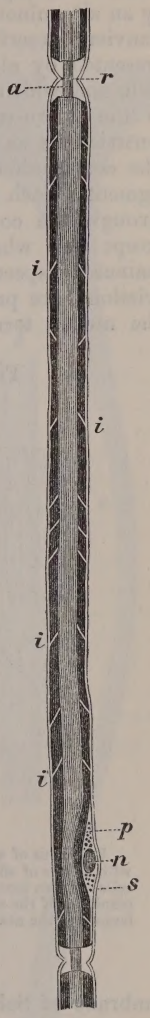
CHAPTER XIII.

OF THE FUNCTIONS OF THE CEREBRO-SPINAL NERVOUS SYSTEM.

1. *General Summary.*

401. The Nervous System of Man, like that of all other Animals, is composed of *ganglionic centres* and *nerve-trunks;* the former being especially composed of 'vesicular substance,' made up of cells which may be spheroidal, fusiform, caudate, stellate, or of almost any variety of shape; the latter consisting entirely of 'nerve-fibres.' If the structure of an ordinary nerve like the Median be examined, it will be found to consist of a framework of connective tissue named the *epineurium*, in which are embedded funiculi, or bundles of nerve fibres of various size. Each of these has its own special sheath of connective tissue, termed the *perineurium*, which is composed of several lamellæ of fibres separated by interlamellary lymph spaces containing a few corpuscles. The funiculi are consequently invested by an epithelium exhibited at Fig. 183, consisting of large flat cells.* On further dissection, the individual fibres are seen to be separated from one another by *endoneurium*, which consists of more or less homogeneous substance, containing numerous minute fasciculi of connective tissue with flattened connective tissue cells. Numerous capillaries, chiefly pursuing a longitudinal course, run in the endoneurium. The living fibres appear as clear, transparent, and highly refractile threads, in which very definite structural characters can be brought into view by the action of various re-agents. After short exposure to the action of air or water, a kind of coagulation occurs, and it then appears that each fibre (Fig. 186) is composed

Fig. 186.

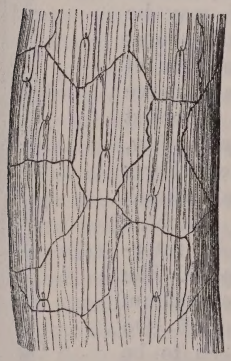


Medullated nerve fibre. *a*, axis-cylinder; *s*, sheath of Schwann; *n*, nerve nucleus, indenting the medullary sheath; *p*, finely granular matter at the poles of the nucleus; *r*, nodes or constrictions of Ranvier, at which point the medullary sheath is interrupted, whilst the axis-cylinder is continued without interruption; *i*, *i*, dissepiments dividing the medullary sheath into segments, corresponding to the inflections of Lantermann.

* Tamamschef, "Centralblatt für die Med. Wiss.," 1872, p. 593, who also gives a comparative table of the action of various re-agents on the cylinder axis and on albumin. See also A. v. Török, "Würzburg Physikal-Med. Verhand.," Band iii. 41, and Key and Retzius, "Studien in der Anatomie des Nervensystems," 1876; Lantermann, "Archiv f. Mic. Anat.," Band xiii. p. 1; Kühnt, idem, p. 427; Hennig, "Dissert. Königsberg," 1877; Ranvier, "Leçons," 1878; Klein and Noble Smith, "Atlas of Histology," p. 84, 1880.

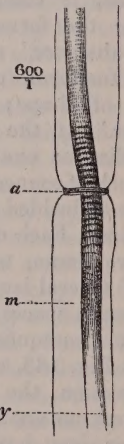
(1) of a very delicate sheath, *the sheath of Schwann*, or neurilemma (s, Fig. 186), within which is an oleaginous material termed the *medullary sheath*, or the white medullary substance of Schwann (2), whilst the core or centre is formed by an albuminous cylindrical thread, the *axis-cylinder*, or primitive band (3). Ranvier* describes certain annular constrictions (Fig. 186, *r*) which are presented by all *medullated* nerve-fibres at intervals of about 1-25th of an inch, and which may be brought into view by means of various re-agents, as the picro-carminate of ammonia and osmic acid. He regards these constrictions as being caused by a thickening of the membrane of Schwann. The constrictions divide the white substance of Schwann into "interannular segments," each containing a nucleus. The axis cylinder runs continuously through the constriction without presenting any trace of segmentation, except that when the fibre is treated with nitrate of silver, it presents a laminated aspect, just above and below the constriction. No such constrictions are presented by the fibres of Remak, or non-medullated fibres. The nuclei, termed also nerve corpuscles (*n*, Fig. 186), lie between the

Fig. 187.



Funiculus of a mouse after impregnation with nitrate of silver. Large flat epithelial cells are seen covering its surface. The explanation of the small crosses is seen by reference to the next figure.

Fig. 188.



Nerve fibre from the sciatic nerve of the rabbit after the action of nitrate of silver. *a*, Ring formed by thickened membrane of Schwann. *m*, White substance of Schwann rendered transparent by glycerin. *Cy*, Axis cylinder, which just above and below the level of the annular constriction presents the striæ of Frommann.

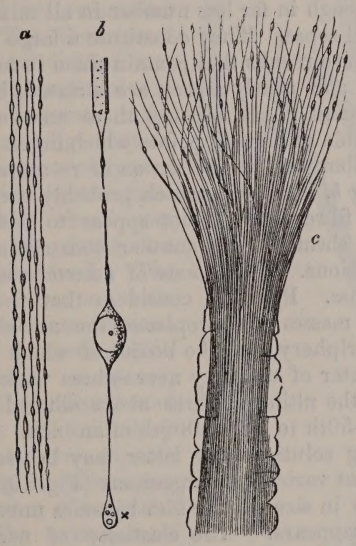
membrane of Schwann and the white substance of Schwann, in which last they are included. They are surrounded by a layer of an albuminoid substance (*p*), which does not stain with osmic acid. In the ganglion cells contained in the brain and spinal cord, and in the ultimate peripheral ramifications of the nerves, both the neurilemma and the white substance of Schwann become indistinct or wholly disappear, whilst the axis cylinder has been observed to break up into fibrils of extreme tenuity, termed elementary or primitive nerve-fibrils;† these are represented in Fig. 190, *c*. The oleaginous

* Brown-Séquard's "Archives de Physiologie," 1872, p. 129, No. 2. Sachs, "Centralblatt," 1873, p. 578.

† See Max Schultze Art. on 'The Histology of the Nervous System,' in the first volume of Stricker's "Human and Comparative Histology," Syd. Soc. Trans., 1870 p. 147.

composition of the white or medullary substance is shown by its ready solubility in ether, and by its blackening with osmic acid. It possesses great refrangibility, is extremely extensible, but inelastic, and of a viscid nature, so that when its continuity is interrupted it has little or no tendency to return to its original position.* In addition to the constrictions of Ranvier, it presents a number of septa† (*i*, *i*, Fig. 186), situated at irregular distances from each other, and dividing it into somewhat funnel-shaped medullary segments. The septa appear to be inflections of the sheath of Schwann. The peculiar appearances pre-

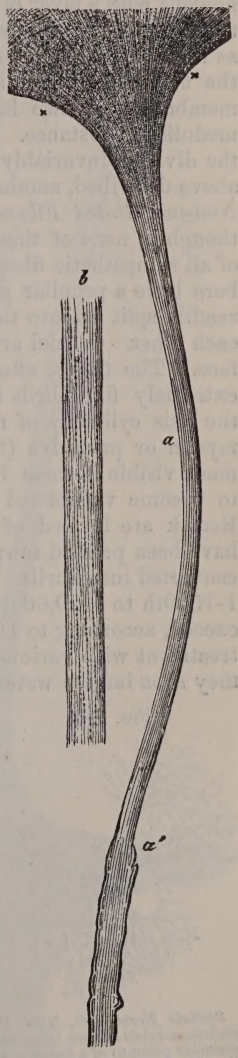
FIG. 190.



Primitive nerve-fibrils. *a*, From the nerve-fibre-layer of the retina. *b*, From the external granular layer of the retina, showing at *x* a larger varicosity, resulting from imbibition. *c*, From the olfactory nerve of the pike, showing a thick nerve inclosed in a sheath breaking up into fibrillæ.

sented by the medullary sheath in polarized light suggest that it consists of, or contains, doubly-refracting bodies (crystalline particles‡), the optic axes of which are arranged radially to the primitive band. The axis cylinder is insoluble in ether, and further differs from the white substance of Schwann in readily staining with carmine. When thus stained it appears in transverse sections to be finely fibrillated and to be surrounded by

FIG. 189.



a, Axis cylinder showing its fibrillar structure; at the upper part *x*, *x*, it is seen to arise from a ganglion cell *a* only partially represented, and to become incrusted by a medullary sheath at *a'*. *b*, Naked axis cylinder, from the dorsal region of the spinal cord of the ox. The medullary sheath has been removed.

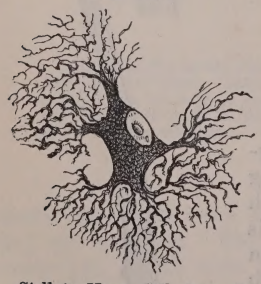
* See Lockhart Clarke's 'Observations on the Structure of Nerve-fibre,' in "Journ. of Med. Sci.," vol. viii. p. 1.

† Lantermann, "Archiv f. Mik. Anat.," Band xiii. 1876; and "Centralblatt f. d. Med. Wiss.," 1876, No. 45; Zawerthal, "Rendic. d. R. Acad. del. Sci. Fis. et Mathemat.," 1874.

‡ Klebs, quoted in Kühne's "Phys. Chemie," 1868, p. 339.

an uncoloured line, which by some* has been regarded as a distinct sheath. Ranvier regards it as a thin layer of protoplasm, in conformity with his view that each interannular segment of nerve-fibre is a fat cell traversed by a special structure, the axis cylinder. On this supposition the neurilemma is the cell wall of the fat cell, and between it and the myelin, or white substance of Schwann, is the nucleus with a layer of protoplasm. The myelin represents the oil globule, and the sheath of the axis cylinder the protoplasm of the fat cell reflected on the axis as in enters the cell. Some observers believe that both the axis-cylinder and the medullary sheath are invested by an extremely delicate keratin or horny membrane, the two layers being connected by oblique septa traversing the medullary substance. The axis cylinder occasionally divides (Beale, Ranvier), the division invariably taking place at a nodal point. In addition to the fibres above described, another kind of nerve fibre, named the *Fibres of Remak, or Non-medullated Fibres*, exists, though in far less number in all mixed nerves, though in none of those of special sense. They constitute a large proportion of all sympathetic fibres. The nerve trunks that contain them in larger numbers have a peculiar greyish red and pearly aspect, are striated, but do not readily split up into their constituent fibres, because these anastomose with each other. Nuclei are discoverable at certain points which lie on their surface. The fibres, after being submitted to the action of re-agents, exhibit extremely fine fibrils (resembling *b*, Fig. 189), which probably correspond to the axis cylinders of medullated fibres, and do not appear to possess either myelin or primitive (Schwann's) sheath. No annular constrictions can be made visible in them by any reactions. Bichromate of ammonia causes them to become vacuolated and varicose. Ranvier† considers that the fibres of Remak are formed of elongated masses of protoplasm, the nuclei of which have been pressed towards the periphery, and the bodies of which have been converted into fibrils. The diameter of ordinary nerve-fibres varies from the 1-1500th to 1-20,000th in., but the ultimate fibres above alluded to do not exceed, according to Dr. Beale, 1-50th to 1-100,000th of an inch. On careful treatment with various hardening solutions, the latter may be isolated, but they soon imbibe water and present varicose enlargements (Fig. 190.) These increase in size till the film becomes unrecognisable and disappears. The elasticity of nerve is the same as that of muscle‡, but its extensibility is less, whilst its cohesion is greater—that is, with the same area of transverse section nerves require a greater weight to extend and rupture them than muscles. The precise mode in which the nerves terminate peripherally can scarcely be said to be accurately known in any instance, with the exception, perhaps, of the Pacinian corpuscles.§ In the case of the motor nerves and of the nerves of special sense, considerable differences of opinion exist (which will be hereafter more particularly referred to), as to whether there is a terminal plexus, or whether the nerves end in loops or in free extremities, or become continuous with gland or muscle-cells. Dr. Klein, in follow-

Fig. 191.



Stellate Nerve Cell, from the nucleus cervicis cornu (posterior vesicular column) of a fœtus of six months × 420.

* Todaro, "Sulla Struttura dei plessi nervoic," Roma, 1872. Kuhnt, "Archiv f. Mic. Anat.," t. xiii. 1876, p. 427.

† Ranvier, "Leçons sur l'Histologie du Système Nerveux," t. I. 1878, p. 153.

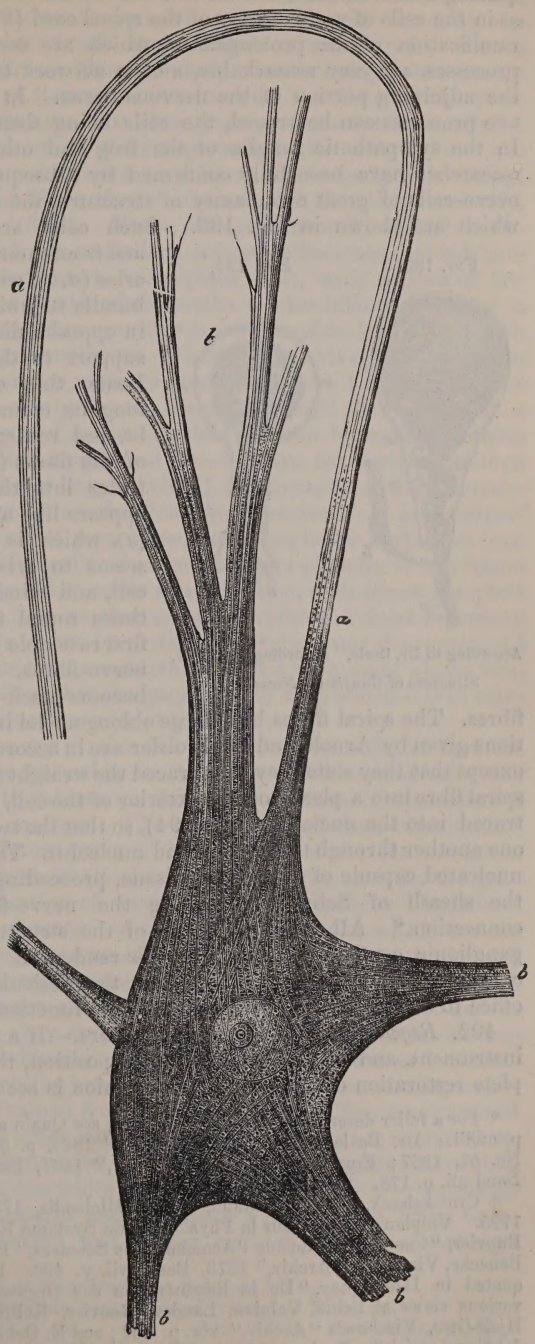
‡ Wertheim, "Annales de Chemie et Physique," Band xxi. 1847, p. 385.

§ See Schäfer, "Quart. Journ. Mic. Sci.," 1875, p. 135; and Arndt, "Centralblatt," 1876, p. 141.

ing out the nerves of the Cornea, seems to have satisfied himself that, in this part at least, the fibres end in free extremities, which run up between the cells on the surface. Nerve fibres are divided into *afferent* or centripetal, which convey impressions to a nervous centre or ganglion; and *efferent* or centrifugal, which conduct impressions from a centre; and central or intramesial Nerves. The Centripetal nerves are subdivided into the sensory nerves and excito-motor nerves, the former conveying impressions which are usually perceived or felt by the individual, while those conveyed by the latter are often unperceived. The Centrifugal fibres are subdivided into motor nerves, distributed to muscles, both striated and unstriated, secretory fibres distributed to glands, and inhibitory nerves, which are capable of arresting or preventing the contraction of muscular tissue. The existence of trophic nerves and of fibres capable of causing active elongation of muscular fibre is still *sub judice*.

Nerve Cells vary much in their form, size, and structure. The simpler kinds are round or oval, the larger polygonal and stellate, (Fig. 191) and it is probable that all possess a nucleus, and give off one, two, or more prolongations, that either intercommunicate with the processes of other cells, or become continuous with the cylinder axis of a nerve-fibre (Fig. 192), gradually ac-

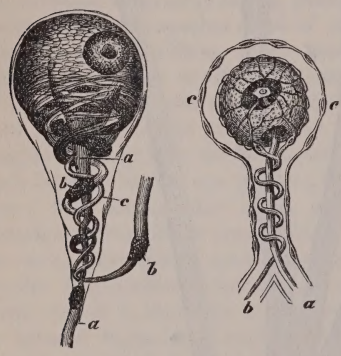
Fig. 192.



A medium-sized ganglion cell from the anterior horn of the grey matter of the spinal cord of a calf isolated after a short maceration in serum containing a little iodine in solution, magnified 600 diam. The processes (as at *b*) are abruptly broken off. *a* is the axis cylinder process.

quiring a neurilemma, and the white substance of Schwann. In some instances, as in the cells of various parts of the spinal cord (Fig. 191), the subdivision and ramification of the prolongations, which are sometimes called protoplasmic processes, are very remarkable, a close network being formed which pervades the adjoining portion of the nervous tissue. In other instances, only one or two processes can be traced, the cells being then termed uni- and bi-polar. In the sympathetic ganglia of the frog and other animals Dr. Beale, whose researches have been fully confirmed by subsequent inquirers, has observed nerve-cells of great complexity of structure, the chief microscopic features of which are shown in Fig. 193. Such cells are pyriform and nucleated, and from their pointed extremity two fibres arise (a, b), which, on reaching the nervous bundle to which they are distributed, run in opposite directions, thus affording some support to the view maintained by Dr. Beale, that every nerve-fibre, however long its course may be, is a loop arising in, and returning to, the same cell. One of the fibres (a) is usually straight, penetrates into the interior of the cell, and appears like a stalk to the cell; the other (b), which is sometimes double at first, seems to arise from the exterior of the cell, and winds spirally for two or three times round the former. Both fibres at first resemble the axis cylinder of ordinary nerve-fibres, and both may subsequently become dark-bordered, or remain pale, fibres. The spiral fibres bear large oblong nuclei in their course. The descriptions given by Arnold and Courvoisier are in accordance with that by Dr. Beale, except that they state they have traced the straight fibre into the nucleus, and the spiral fibre into a plexus on the exterior of the cell, but which may ultimately be traced into the nucleolus (Fig. 194), so that the two fibres are continuous with one another through the nucleus and nucleolus. The whole cell is invested by a nucleated capsule of connective tissue, proceeding from and continuous with the sheath of Schwann investing the nerve-fibres with which it is in connection.* All our knowledge of the structure and endowments of the ganglionic centres and nerve-trunks renders it probable that they bear a *complementary* relation to each other; the Vesicular substance having for its office to *originate* changes, which it is the function of the Fibrous to *conduct*.

Fig. 193. Fig. 194.



According to Dr. Beale. According to Arnold.

Structure of *Ganglionic Nerve-Cell.*

402. *Regeneration of Nervous Structure.*—If a nerve be divided by a sharp instrument, and the ends placed in apposition, they will reunite, with complete restoration of function.† The union is accomplished by the effusion of

* For a fuller description of these structures, see Quain and Sharpey's "Introd. to Anat.," p. cxliii.; Dr. Beale, "Philosoph. Transact.," 1863, p. 543; Courvoisier, "Centralblatt," No. 57, 1867; Frantzel, Virchow's "Archiv," 1867, Band xxxviii. p. 549; Arnold, Id., Band xli. p. 178. Schultze, loc. cit.

† Cruickshank, 1776. Fontana, 1778. Michaelis, 1785. Haighton, "Phil. Trans.," 1795. Vulpian, "Leçons sur la Physiologie du Système Nerveux," Paris, 1866. Forscher, Ranvier, "Comptes Rendus de l'Académie des Sciences," 1873, p. 491, and t. lxxv. p. 1831. Benecke, Virchow's "Archiv," 1873, Band lvii. p. 496. Laveran, 'Thèse de Strasbourg,' quoted in Demarquay, "De la Régénération des Organes et des Tissues," in which the various views of Schiff, Vulpian, Landry, Ranvier, Kölliker, and others are well given. Hjelt-Otto, Virchow's "Archiv," xix. p. 352; and E. Oehl, "Sul processo di Rigenerazione del Nervi recisi." Pavia, 1864, 8vo.

gelatinous lymph, in which connective tissue and elastic fibres form, by which the continuity of the perineurium is restored. According to some, bipolar cells are developed within this sheath, the processes of which unite to form the axis-cylinders of new nerves; the medullary sheath being subsequently developed around them. But Ranvier maintains that the fibres of the peripheric stump atrophy, and that the new fibres proceed from the axis cylinder of the centric stump, which make their way through the cicatrix *into* the degenerated fibres, or run in the connective tissue of the peripheric stump. The changes that occur in the fibres after section are, that they become cloudy, and their margins are less defined. These changes are well marked on the eighth day, soon after which the medullary substance becomes divided into segments, and a kind of coagulation takes place in it, with deposit of fat-globules. In the course of a month or six weeks the medullary substance is reduced to a mass of extremely fine granular molecules of fat-like dust, which finally disappear, and the sheaths collapse. Whether the axis cylinders remain for a long time unaltered,* or also undergo absorption, is still doubtful. The time that elapses before the newly-formed tissue can fulfil the function of a nerve in transmitting sensory and motor impulses is given by various authors at from 7—15 days for the first traces, and 30—90 days for complete return of sensation and motion.† According to Schiff,‡ regeneration of the pneumogastrics may occur even when two inches have been excised. It is questionable whether, after extirpation of a ganglion, new ganglionic corpuscles can be formed; yet, in Brown-Séquard's experiments upon pigeons, it was found that the whole spinal cord would re-unite after division, with almost complete restoration of function. It is to be observed that whilst the distal extremity of a nerve separated from its centre by section undergoes fatty degeneration,§ the proximal portion retains for a considerable period its normal characters, indicating, according to Waller, that the ganglion cell with which it is in relation exercises a certain influence over its nutrition.

403. As regards the *chemistry* of the Nerves, it has been found that the Brain contains about 75 per cent. of water, and 25 of solid residue, of which about 15 parts consist of fatty substances, 7·5 of albuminous compounds, 1·5 of salts, and 1 of extractive matters. The proportions of these constituents, however, are different in different parts of the nervous system; the amount of water, for instance, varying from 70 (in the white) to 85 per cent. (in the grey substance). The large proportion of water may be supposed, as Thudichum suggests, to permit freedom of motion of the ultimate particles within certain limits. It also promotes active changes of nutrition by the penetration of new matter by diffusion, and the rapid removal of effete crystallizable material. The albuminous compounds are chiefly contained in the axis cylinder and in the protoplasm of the cells; they appear to consist of a substance resembling myosin, globulin, and alkali-albumin. Amongst the albuminous are, nuclein and a substance closely resembling kerato-neurin, named kerato-elastin, a substance similar to which is obtained from Schwann's sheath. The fat contained in the grey matter is always much smaller in quantity than that in the white. According to Petrowsky,‖ when dried the grey substance contains more than half of its weight of albumin, the white only one-quarter. The grey substance (dried) contains 18·7 of Cholesterin and fat, and 0·5 of a fat-like body, Cerebrin, the white 51·9 of Cholesterin, and 9·5 per cent. of Cerebrin. Amongst

* "Comptes Rendus de l'Académie des Sciences," Mars 6, 1854.

† Descot, "Thèse Inaugurale," 1822; Paget, "Surgical Pathology."

‡ Vierordt, "Physiologie," 1861, p. 44. § See Schiff, "Physiologie," p. iii.

‖ Pflüger's "Archiv," 1873, p. 369.

the chief constituents of the cerebral substance, in addition to Cerebrin, is Lecithin, with the products of its decomposition—viz., glycerin-phosphoric and oleo-phosphoric acids, neurin or cholin ($C_5H_{15}NO_2$), a strongly alkaline colourless fluid forming salts with acids, and other fat-like substances containing phosphorus and soluble in ether; palmitic acid, small quantities of ordinary fat, and volatile fatty acids. Besides these, an albuminous substance resembling Myosin, a substance analogous to Elastin, small quantities of a soluble albuminous substance, coagulating at 147° F., have been found, together with Nuclein, Inosit, Sarkin, Xanthin, Kreatin; Lactic, Uric, and Phosphoric acids, and their combinations with Potash, Lime, and Magnesia; Silicic Acid, Oxide of Iron, Fluorine, small quantities of Alkaline Sulphates, and lastly, Chloride of Sodium.* The quantity of Phosphorus is very large, amounting, according to Borsarelli,† to from 1·352 to 1·790 per cent. Perfectly fresh nerves, when at rest, possess a neutral or perhaps slightly alkaline reaction.‡ According to Ranke, they become acid after tetanus. The white substance of the brain and spinal cord is feebly alkaline or neutral. After exhausting work and after death it is acid. The grey substance is always acid.§

404. As regards the general relations of the principal Centres of the Nervous System of Man, it is only requisite here to remark, that those which make up the Cerebro-Spinal portion of the apparatus have such an intimate structural relation to each other, and so much more frequently act consentaneously than separately, that, notwithstanding the abundant evidence of the diversity of their respective endowments, there is considerable difficulty in the determination of their special functions; since the destruction or removal of any one portion of the Nervous system, not only puts a stop to the phenomena to which that portion is directly subservient, but so deranges the general train of nervous activity, that it often becomes impossible to ascertain, by any such method, what is its real share in the entire performance.—In this difficulty, however, we may advantageously have recourse to the study of the structure and actions of those forms of the Nervous System presented to us among the lower animals, in which its ganglionic centres are fewer and less intimately connected, and in which, therefore, it is more easy to gain an acquaintance with their several endowments. And from an extensive survey of these, we seem able to deduce the following conclusions, which afford the most valuable guidance in the study of the Nervous System of Man :‖—

I. The Nervous System, in its lowest and simplest form, may consist of but a single ganglionic centre,¶ with afferent and motor nerves, whose function is essentially *internuncial;* impressions made upon the afferent fibres exciting respondent or "reflex" movements in the muscles supplied by the motor, without any necessary intervention of consciousness.—Such movements are properly distinguished as *excito-motor.*

II. A simple repetition of such ganglionic centres may exist to any extent, without heterogeneousness of function, or any essential departure from the

* v. Gorup Besanez, "Phys. Chemie," 1875, p. 697. † "Syd. Soc. Year-book," 1861, p. 32.

‡ See Heidenhain, "Studien des Phys. Instit. zu Breslau," 1868, p. 248; and Liebreich, in "Tageblatt der Natur-forsch. Versammlung zu Frankfürt," 1867.

§ Gscheidlen, "Archiv f. Physiol.," Band viii. 1873, p. 172.

‖ For a general view of the facts on which these conclusions are based, see "Princ. of Comp. Phys.," chap. xiii.

¶ It may, perhaps, be doubted whether any Animal really exists possessing such a nervous system, and yet not endowed with consciousness. It is quite certain, however, that animals do exist (the Tunicata, for example, which are probably examples of degradation. See Lankester, "On Degeneration," 1880,) in which the actions above referred to are the only ones of which we have any distinct evidence from observation of their habits.

mode of action just indicated; each of these centres may be specially connected by afferent or motor fibres with one segment or division of the body, and may minister peculiarly to *its* actions; but the several centres may be so intimately connected by commissural fibres, that an impression made upon the afferent nerves of any one of them may excite respondent motions in other segments. —This we see effected through the annular gangliated cord of the higher Echinodermata and through the longitudinal g angliated cord of the Arthropods; the disposition of the ganglia and of their connecting cords having reference simply to the general plan of the body.

III. A higher form of the Nervous System is that in which the multiplication of similar parts which are to be alike supplied with nervous power, but to the exercise of a diversity of functions, through the instrumentality of different structures: thus, in the higher Arthropoda and in some of the Mollusca we find ganglionic centres specially set apart for the actions of deglutition and respiration, as well as for those of locomotion; but their *modus operandi* is still the same, these actions being all 'excito-motor,' that is, being performed through the 'reflex' agency of their several ganglionic centres, without the necessary intervention of consciousness. These centres are connected with each other commissurally, when they are required to act with consentaneousness; and it is frequently to be observed in the most developed forms of each type, that they come into actual coalescence, their functional distinctness being still indicated, however, by the distribution of their nerve-trunks.

IV. In all but the very lowest Invertebrata, the Nervous System includes, in addition to the foregoing, certain ganglionic centres, situated in the neighbourhood of, or the entrance to, the digestive cavity, and connected with organs, which, from their more or less close resemblance to our own instruments of special sense, we conclude to be organs of sight, smell, hearing, &c. Now, as we know from our own experience that impressions made upon these organs produce no influence on our actions unless we become *conscious* of them, and as the Invertebrata possess no distinct ganglionic centres of a higher character, it seems to be a legitimate inference, that these 'sensorial' ganglia are the instruments by which the animals furnished with them are rendered cognizant of such impressions, and through which the sensations thus called into existence serve to prompt and direct their movements. What is commonly designated as the 'brain' of Invertebrata (more properly their 'cephalic ganglia') cannot be shown to consist of anything else than an assemblage of *sensorial* centres; and its actions appear to be entirely of a 'reflex' character, such of the movements of these animals as are not excito-motor, being performed (there is strong reason to believe) in direct respondence to sensations excited by internal or external impressions. Such movements, therefore, may be designated as *sensori-motor* or *consensual*. Like the preceding, they do not appear to involve the participation either of Emotion, Reason, or Will; and the proportion which they bear to the actions of the excito-motor kind, seems to correspond pretty closely with the relative development of the cephalic ganglia and of the rest of the nervous system, as is very obvious when the larva and imago states of Insects are compared.— However disjointed the various 'excito-motor' centres may be amongst each other, we uniformly find them connected with the 'sensory' ganglia by commissural tracts; and this anatomical fact, with many phenomena which observation and experiment upon their actions have brought to light, makes it apparent, that besides the reflex actions which are performed through their own direct instrumentality, the sensory ganglia have a participation in those performed through other ganglionic centres. Thus it seems probable that a

stimulus transmitted downwards from the sensory ganglia, to one of the ganglia of the trunk of a Centipede, excites the efferent nerves of that ganglion to call into contraction the muscles supplied by them, just as the excitor influence arriving at that ganglion through its own afferent nerves would do.

405. The whole Nervous System of Invertebrate Animals, then, may be regarded as ministering entirely to *purely-reflex* action; and its highest development, as in the class of Insects, is coincident with the highest manifestations of the 'instinctive' powers, which, when carefully examined, are found to consist entirely in movements of the excito-motor and sensori-motor kinds. When we attentively consider the habits of these animals, we find that their actions, though evidently adapted to the attainment of certain ends, are very far from evincing a *designed* adaptation on the part of the beings that perform them, such as that of which we are ourselves conscious in our own voluntary movements, or which we trace in the operations of the more intelligent Vertebrata. For, in the first place, these actions are invariably performed in the same manner by all the individuals of a species, when the conditions are the same; and thus are obviously to be attributed rather to a uniform impulse, than to a free choice; the most remarkable examples of this being furnished by the economy of Bees, Wasps, and other 'social' Insects, in which every individual of the community performs its appropriate part, with the exactitude and method of a perfect machine. The very perfection of the adaptation, again, is often of itself a sufficient evidence of the unreasoning character of the beings which perform the work; for, if we attribute it to their own intelligence, we must admit that this intelligence frequently equals, if it does not surpass, that of the most accomplished Human reasoner.* Moreover, these operations are performed without any guidance from experience; for it can be proved in many cases that it is impossible for the beings which execute them to have received any instruction whatever; and we see that they do not themselves make any progressive attempts towards perfection, but that they accomplish their work as well when they first apply themselves to it, as after any number of repetitions of the same acts. It is interesting to observe, moreover, that as these instinctive operations vary at different periods of life, so there is a corresponding variation in the structure of the Nervous system. Thus we see that, in the *larva* of the Insect, these operations are entirely directed towards the acquisition of food; and its organs of sense and locomotive powers are only so far developed as to serve this purpose. But in the *imago* or perfect Insect, the primary object is the continuance of the race; and the sensorial and motor endowments are adapted to enable the individual to seek its mate, and to make preparations (frequently of a most elaborate kind) for the nurture of the offspring.—Hence we can scarcely fail to arrive at the conclusion, that the *adaptiveness* of the instinctive operations of Insects, &c., lies in the original construction of their nervous system, which causes particular movements to be executed in direct respondence to certain impressions and sensations. And this view is confirmed by the comparison of such movements with those which, in the Human subject, are most directly concerned in the maintenance of the life of the individual, and in the perpetuation of the race. For we have the evidence of our own consciousness in regard to these, that, however obvious their *purpose* may be, and however complete their *adaptation* to that purpose, they are performed, *not* with any notion of that purpose, but at the prompting of an irresistible impulse which is not only independent of all intelligent appreciation of the result, but may produce its effect without even

* See "Princ. of Comp. Phys.," 4th edit., p. 695.

affecting the consciousness of the agent. Thus the infant seeks the nipple, and puts its muscles into suctorial action, without any knowledge, derived from experience, that by so doing it will relieve the uneasy feeling of hunger; and if we could imagine a man coming into the world with the full possession of all his faculties, we may feel tolerably certain that he would not wait to eat until he had learnt by experience his dependence upon food. We shall see that adult animals whose Cerebral hemispheres have been removed, will eat food that is put into their mouths, although they will not go to seek it; and this is the case with many Human idiots. When the functions of the Brain are destroyed, or in partial abeyance, as in fever, we often observe a remarkable return to the instinctive propensities in regard to food; and the physician frequently derives important guidance with respect to the patient's diet and regimen (particularly as to the administration of wine), from the inclination or disinclination which he manifests. So, in regard to the intercourse of the sexes, the impulse which prompts to it does not arise from a knowledge of the ultimate purposes which it is designed to answer; and the higher powers of the mind are only so far concerned in it, that when the action of the instinctive impulse has led to the formation of a definite idea of the object of desire, the intelligence is prompted to take means for its gratification.*

406. Thus, then, the type of psychical perfection among Invertebrate animals, which is manifested in the highest degree in the Social Insects, consists in the exclusive development of the Instinctive faculty—that is, of *automatic* powers of a very simple kind; in virtue of which, each individual performs those actions to which it is directly prompted by the impulses arising out of impressions made upon its afferent nerves, without any self-control or self-direction; so that it must be regarded as entirely a creature of necessity, performing its instrumental part in the economy of Nature, from no design or will of its own, but in accordance with the plan originally devised by its Creator.

407. On turning to the Vertebrate series, on the other hand, we find that *its* type of psychical perfection—as shown in Man—consists in the highest development of the *Reason*, and in the supreme domination of the *Will*, to which all the 'automatic' actions, save those which are absolutely essential to the maintenance of the Organic functions, are brought under subjection; so that each individual becomes not only a thinking and reflecting, but a self-moving and self-controlling agent, whose actions are performed with a definite purpose which is distinctly before his own view, and are adapted to the attainment of their end by his own intelligence. This, however, is only true of Man in his most elevated state; and not only in ascending the Vertebrate scale, but also in watching the progressive evolution of *his* mental faculties during the earlier periods of his life, may we trace a regular gradation from a condition but little (if at all) in advance of that of the higher Invertebrata, up to that which is displayed in the noblest examples of Humanity. Through the entire series, however, we perceive that the Excito-motor and Sensori-motor portion of the Nervous system constitutes its fundamental and essential part; serving not merely as the instrument whereby those actions

* We have not, perhaps, any right to affirm that there is *nothing whatever* analogous in the Invertebrata to the Reasoning powers and Will of higher animals; but if these faculties have any existence among them, they must be regarded as in a merely rudimentary state, corresponding with the undeveloped condition of the Cerebrum. The only distinct indication of intelligence displayed by Invertebrata, is the slight degree of capacity of "learning by experience" which some of them display; this capacity being limited to the mere formation of *associations* between the psychical called-up by different objects of sense, which we observe to be the first stage in the development of the mental powers in the Human infant.

are performed, which are as necessary among the higher animals as they are among the lower, for the maintenance of the Organic functions; but also as the immediate recipient of all those impressions from without, by which the higher operations of Mind are excited, and as the executant of the actions which proceed from them. But as we ascend the Vertebrate scale, or as we watch the progressive psychical development of the Infant, we find it becoming more and more obvious that the actions are prompted, not so much by simple sensations, as by *ideas* or notions of the objects to which they relate; these ideas being founded, in a large proportion of instances, upon the results of past experience, and the course of action being shaped in accordance with it. In the acts of animals of a still higher grade, as in those of the Child, we can scarcely fail to perceive the manifestation of *reasoning processes* analogous to those which we ourselves perform, and the expressions of some of those *emotional states* of which we are ourselves conscious. The superaddition of these more elevated endowments, in the Vertebrate series, is coincident with the addition of a peculiar ganglionic centre, the *Cerebrum*, to the Sensori-motor apparatus; and the relative proportion which the former bears to the latter, both as to size and to complexity of structure, corresponds so closely with the degree of predominance which the Intelligence possesses over the Instinctive propensities, that it is scarcely possible to doubt that the Cerebrum is the instrument through which this higher form of psychical power is exercised. Much of this exercise, however, may still be *automatic* in its nature; for so long as the current of thought and feeling flows on in accordance with the direct promptings of Suggestion, and without any interference from Volition, may it be considered as a manifestation of the 'reflex' activity of the Cerebrum, which takes the form of a *mental instinct*. This reflex activity manifests itself not only in the psychical operations themselves, but also in muscular movements; and these, when they proceed from simple ideas without any excitement of feeling, may be designated as *ideo-motor:* whilst if they spring from a passion or emotion, they are termed *emotional*. The *mental* instincts, however, are by no means as invariable in the different individuals of the same species, as are what may be termed the *physical* Instincts of that inferior part of the nervous apparatus, which is more closely connected with the maintenance of the Organic life; the particular changes which any given suggestions will excite in each, being partly determined by original constitution, and partly by acquired habits.

408. The superiority of the Mind of Man over that of the most elevated among the lower animals, consists not only in the far greater variety and range of his faculties, but yet more in that dominant power of the Will which enables him to utilize them with the highest effect. In so far as the course of his thoughts and feelings is the mere result of the action of external impressions upon an organization having certain respondent tendencies, must he be considered as irresponsible for his actions, his character being formed *for* instead of *by* him: but in so far as he can exert a Volitional power of directing his thoughts and controlling his feelings, may he rise superior to circumstances, make the most advantageous use of the Intellectual faculties with which he may be endowed, and bring his Moral character more and more into accordance with the highest type which his nature may be capable of attaining in its present sphere of existence. Notwithstanding the evidences of rationality which many of the lower animals present, and the manifestations which they display of emotions that are similar to our own, there is no ground to believe that *they* have any such controlling power; on the contrary, all observation seems to lead to the conclusion that they are under the complete domination

of the ideas and emotions by which they may be for the time possessed, and have no power either of repressing these by a forcible act of Will, or of turning the attention, by a like voluntary effort, into another channel. In this respect, then, their condition resembles that of the Dreamer, the Somnambule, or the Insane patient, in all of whom this voluntary control is suspended, and who (when their minds are susceptible of external impressions) may be so 'played upon' by the suggestion of ideas, that any respondent action consistent with the ordinary mental state of the individual may be evoked by an appropriate stimulus; just as we see in the case of animals that are trained to the performance of particular sets of movements, which are executed in respondence to certain promptings conveyed to them through their sensorium. Now between the complete want of this controlling power of the Will, and the most perfect possession of it, every intermediate gradation is presented by the several individuals which make up the Human species; some persons being so much accustomed, in consequence of the weakness of their Will, to act directly upon the prompting of every transient impulse, that they can scarcely be said to be voluntary agents; and others allowing certain *dominant* ideas or *habitual* feelings to gain such a mastery over them, as to exercise that determining power which the Will alone ought to exert. This gradation may be perfectly traced in children, in whose education the development of the faculty of 'self-control' should be a leading object; and it is also displayed in certain phases of mental Imbecility, which result from a deficiency of the power of voluntarily fixing the attention upon any object of consciousness, and of thus withdrawing it either from external objects that tend to distract the mind, or from notions it has adopted which hold it in subjection.

409. When we apply ourselves to the study of the Cerebro-Spinal Nervous Centres of Man, we find ourselves peculiarly liable to be misled by the great development which the Cerebrum presents, both as to size and to complexity of structure, in proportion to the other centres; and thus it has happened that, through the too exclusive attention commonly paid to *Human* Anatomy, the meaning of the facts brought to light by dissection has been very commonly misapprehended, and many of the physiological interpretations based upon them have been completely negatived by more extended inquiry.—It is only, in fact, by studying the Cerebro-Spinal apparatus in its lowest, as well as in its highest, form, and by bringing the intervening grades into comparison with both extremes, that it is possible to establish what are its fundamental or essential, and what its accessory, parts; and in this way only can such a correspondence be established between the development of a particular structure and the manifestation of a psychical endowment, as may enable the latter to be attributed with any degree of probability to the former. In fact, there is no part of the Human Organism, as to which the advantages of such a comparison are so striking, or in which the value of the "experiments ready prepared for us by Nature" is so much above that of the results of artificial mutilations.

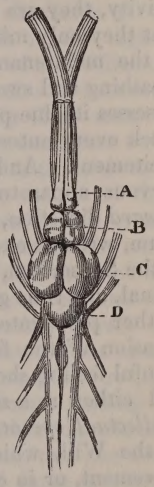
410. *Cerebro-Spinal Nervous Centres.*—Under the guidance, then, of these principles, we find that we may distinguish, as the fundamental part of the Cerebro-Spinal Apparatus of Man, the *Cranio-Spinal Axis*, consisting of the Spinal Cord, the Medulla Oblongata, and the Sensory Ganglia, and altogether constituting the centre of automatic movement.—The Spinal Cord, consisting of a tract of vesicular matter enclosed within strands of longitudinal fibres, and giving off successive pairs of intervertebral nerves which are connected at their roots with both of these components, it is obviously homologous with the gangliated ventral column of the Arthropoda, chiefly differing from it in the continuity of the ganglionic substance which occupies its interior; and each

segmental division of it, which serves as the centre for its own pair of nerves, may be considered, like each ganglion of the ventral column of the Arthropoda, as a repetition of the single 'pedal' or locomotive ganglion of the Mollusca. —The Medulla Oblongata consists of a set of strands, which essentially correspond with the cords that pass round the œsophagus in Invertebrate animals, connecting the cephalic ganglia with the first sub-œsophageal ganglion; but as the whole cranio-spinal axis in the Vertebrata lies *above* the alimentary canal (the trunk being supposed to be in a horizontal position), there is no such divergence of these strands, the only separation between them being that which is known as the 'fourth ventricle.' Interposed among the commissural fibres of the Medulla Oblongata, however, are certain collections of vesicular matter, which serve as the ganglionic centres, governing the calibre of the vessels, and for the movements of respiration and deglutition, the latter corresponding with the 'respiratory' and 'stomato-gastric' ganglia of Invertebrate animals. This incorporation of so many distinct centres into one system, would seem destined in part to afford to all of them the protection of the vertebral column; and in part to secure that consentaneousness of action and that ready means of mutual influence, which are peculiarly requisite in beings in whom the activity of the Nervous system is so predominant. Thus the close connection which is established in the higher Vertebrate animals between the respiratory and the general locomotive apparatus, is obviously subservient to the use which the former makes of the latter in the performance of its functions; whilst, on the other hand, the control which their encephalic centres possess over the actions of the respiratory ganglia, enables the Will to regulate the inspiratory and expiratory movements in the manner required for the acts of vocalization.—Under the term Sensory Ganglia, may be comprehended that assemblage of ganglionic masses lying along the base of the skull in Man, and partly included in the Medulla Oblongata, in which the nerves of the 'special senses,' Taste, Hearing, Sight, and Smell, have their central terminations; and with these may probably be associated the two pairs of ganglionic bodies known as the Corpora Striata and Thalami Optici, into which may be traced the greater proportion of the fibres that constitute the various strands of the Medulla Oblongata, and which seem to stand in the same kind of relation to the nerves of Touch or 'common sensation,' that the Olfactive, Optic, Auditory, and Gustative ganglia bear to *their* several nerve-trunks.

411. Now it is not a little interesting that this Cranio-Spinal axis, which represents in Vertebrate animals the whole nervous system of the Invertebrata (with the exception of the rudiment of the Sympathetic which they possess), should exist in the lowest known Vertebrate animal without any superaddition, and should be sufficient for the performance of all its actions. Such is the case in the curious *Amphioxus*, a little fish which presents not the slightest trace of either Cerebrum or Cerebellum, and in which even the sensory ganglia and the organs of special sense have only a rudimentary existence; and in which, too, the spinal cord is composed of a series of ganglia that are obviously distinct from each other, although in close approximation. And even in the lower Cyclostome Fishes, the condition of the nervous centres is very little above this, save as regards the larger development of the sensory ganglia.—This condition has its parallel, even in the Human species, in the case of Infants which are occasionally born without either Cerebrum or Cerebellum; such have existed for several hours, or even days, breathing, sucking, crying, and performing various other movements; and there is no physiological reason why their lives should not be prolonged, if they be nurtured with sufficient care.

412. In Man, however, as in all the higher Vertebrata, we find superimposed (as it were) upon the Sensory ganglia, and constituting the principal mass of the Encephalon, the bodies which are known as the *Cerebral Hemispheres*, or *Hemispheric Ganglia*. Now when these are so greatly developed as to cover-in and obscure the Sensory ganglia to the degree which presents itself in Man, it is not surprising that the fundamental importance of the latter should not be generally recognized; in Fishes, however, the proportion between the two sets of centres is entirely reversed, the rudiments of the Cerebral Hemispheres (Fig. 195, B) being usually inferior in size to the Optic ganglia (C) alone. Indeed, of the pair of ganglionic masses to which that designation is usually applied, it may be almost positively stated that the greater part is homologous with the Corpora Striata of the Human Brain; it being only in the higher Cartilaginous fishes that a ventricular cavity exists in each of these bodies, separating the thin layer of true Cerebral substance which overlies it from the ganglionic mass which forms its floor. Between these two extremes, a regular gradation is presented in the intermediate tribes.—Now it is a point especially worthy of note, that no sensory nerves terminate directly in the Cerebrum, nor do any motor nerves issue from it; and there seems a strong probability that there is *not* (as formerly supposed) a direct continuity between all or even any of the nerve-fibres distributed to the body, and the Medullary substance of the Cerebrum. For whilst the nerves of 'special' sense have their own ganglionic centres, it cannot be shown that the nervous fibres of 'general' sense, which either enter the cranium as part of the cephalic nerves, or which pass up from the Spinal cord, have any higher destination than the Thalami Optici. So the motor-fibres which pass forth from the Cranium, either into the cephalic nerve trunks, or into the motor columns of the Spinal cord, though commonly designated as *Cerebral*, cannot be certainly said to have a higher origin than the Corpora Striata. And we shall find strong physiological as well as anatomical ground for the belief, that the Cerebrum has no communication with the external world, otherwise than by its connection with the Sensori-motor apparatus; and that even the movements which are usually designated as 'voluntary,' are only so as regards their original source, the stimulus which calls the muscles into contraction being even then immediately issued from the Cranio-Spinal axis, as it is in the movements prompted by the reflex stimulation of an external impression.

Fig. 195.



Brain of *Cod*:—A, olfactive ganglia; B, cerebral lobes; C, optic ganglia; D, cerebellum.

413. Wherever a Cerebrum is superimposed upon the Sensory Ganglia, we find another ganglionic mass, the *Cerebellum*, superimposed upon the Medulla Oblongata. The development of this organ bears a general, but by no means a constant, relation to that of the Cerebrum: for in the lowest Fishes it is a thin lamina of nervous matter on the median line, only partially covering in the 'fourth ventricle;' whilst in the higher Mammalia, as in Man, it is a mass of considerable size, having two lateral lobes or hemispheres in addition to its central portion. The direct communication which the Cerebellum has with both columns of the Spinal cord, and the comparatively slight commissural connection which it possesses with the higher portions of the

Encephalic centres, justify the supposition that it is rather concerned in the regulation and co-ordination of the actions of the former, than in any proper psychical operations; and it will hereafter be shown that the various kinds of evidence afforded by Comparative Anatomy, by Experimental inquiry, and by Pathological observation, all tend to support this view of its function.

414. Now although every segment of the Spinal Cord, and every one of the Sensory Ganglia, may be considered, in common with the Cerebrum, as a true and independent centre of nervous power, yet this independence is only manifested when these organs are separated from each other; either structurally—by actual division; or functionally—by the suspension of the activity of other parts. In their state of perfect integrity and complete functional activity, they are all (at least in Man) in such subordination to the Cerebrum, that they only minister to *its* actions, except in so far as they are subservient to the maintenance of the Organic functions, as in the automatic acts of breathing and swallowing. With regard to every other action, the Will, if it possesses its due predominance, can exercise a determining power; keeping in check every automatic impulse, and repressing the promptings of emotional excitement. And this seems to result from the peculiar arrangement of the nervous apparatus; which causes the excitor *impression* to travel in the *upward* direction, if it meet with no interruption, until it reaches the Cerebrum, without exciting any reflex movements in its course. When it arrives at the Sensorium, it makes an impression on the consciousness of the individual, and thus gives rise to a *sensation;* and the change thus induced, being further propagated from the sensory ganglia to the Cerebrum, becomes the occasion of the formation of an *idea.* If with this idea any pleasurable or painful feeling should be associated, it assumes the character of an *emotion:* and either as a simple or as an emotional idea, it becomes the subject of *intellectual operations*, whose final issue is in a *volitional determination*, or act of the Will, which may be exerted in producing or checking a muscular movement, or in controlling or directing the current of thought.

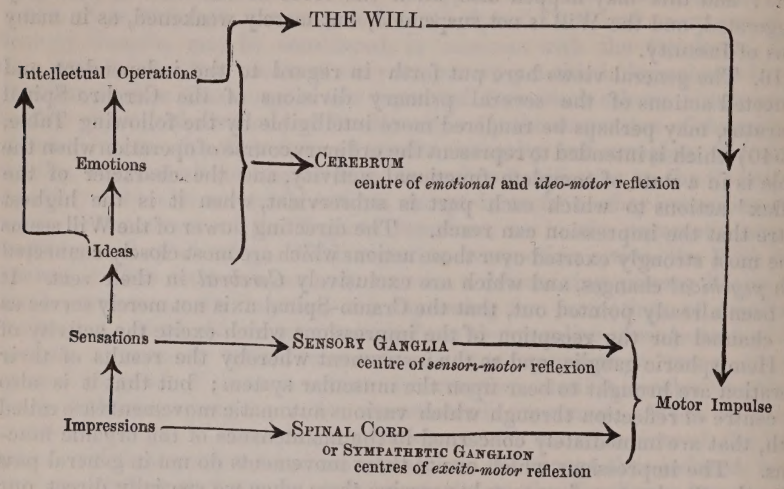
415. But if this ordinary upward course be anywhere interrupted, the impression will then exert its power in a *transverse* direction, and a 'reflex' action will be the result; the nature of any reflex act being dependent upon the part of the Cerebro-Spinal axis at which its ascent had been checked. Thus if the interruption be produced by such division or injury of the Spinal Cord that its lower part is cut off from communication with the encephalic centres, this portion then acts as an independent centre; and impressions made upon it through the afferent nerves proceeding to it from the lower extremities, excite violent reflex movements, which, being thus produced without sensation, are designated as 'excito-motor.'—So, again, if the impression should be conveyed to the Sensorium, but should be prevented by the removal of the Cerebrum, or by its state of functional inaction, or by the direction of its activity into some other channel, from calling forth ideas through the instrumentality of the latter, it may act upon the motor apparatus by the 'reflex' power of the Sensory ganglia themselves; as seems to be the case with regard to those locomotive actions which are maintained and guided by sensations during states of profound abstraction, when the attention of the individual is so completely concentrated upon his own train of thought, that he does not *perceive* external objects, although his movements are obviously guided through the visual and tactile senses. Such actions being dependent upon the prompting of sensations, are 'sensori-motor' or 'consensual.'—But further, even the Cerebrum responds automatically to impressions fitted to excite it to 'reflex' action, when from any cause the Will is in abeyance, and its power

cannot be exerted either over the muscular system or over the direction of the thoughts. Thus in the states of Reverie, Dreaming, Somnambulism, &c., whether spontaneously or artificially produced, *ideas* which take possession of the mind, and from which it cannot free itself, may excite respondent movements; and this may happen also when the force of the Idea is morbidly exaggerated, and the Will is not suspended, but merely weakened, as in many forms of Insanity.

416. The general views here put forth in regard to the independent and connected actions of the several primary divisions of the Cerebro-Spinal apparatus, may perhaps be rendered more intelligible by the following Table, (p. 540) which is intended to represent the ordinary course of operation when the whole is in a state of complete functional activity, and the character of the 'reflex' actions to which each part is subservient, when it is the highest centre that the impression can reach. The directing power of the Will seems to be most strongly exerted over those actions which are most closely connected with *psychical* changes, and which are exclusively *Cerebral* in their seat. It has been already pointed out, that the Cranio-Spinal axis not merely serves as the channel for the reception of the impressions which excite the activity of the Hemispheric ganglia, and as the instrument whereby the results of their operation are brought to bear upon the muscular system; but that it is also the centre of reflection through which various automatic movements are called forth, that are immediately concerned in the maintenance of the organic functions. The impressions which excite these movements do not in general pass on to the Cerebrum; for we only perceive them when we specially direct our attention to them, or when they exist in unusual potency. Thus we are unconscious of the 'besoin de respirer' by which our ordinary movements of respiration are prompted; and it is only when we have refrained from breathing for a few seconds, that we experience a sensation of uneasiness which impels us to make forcible efforts for its relief. Notwithstanding, however, that the Cerebrum is thus unconcerned in the ordinary performance of those automatic movements, yet it can exert a certain degree of control over many of them, so as even to suspend them for a time, though in no instance can it carry this suspension to such an extent as seriously to disarrange the Organic functions; thus, when we have voluntarily refrained from breathing for a few seconds, the inspiratory impulse so rapidly increases in strength with the continuance of the suspension, that it at last overcomes the most powerful effort we can make for the repression of the movements to which it prompts. Now in this and similar cases it would seem as if the Will interfered to prevent that direct transverse passage of the stimulus from the afferent to the efferent nerves through the Cranio-Spinal axis, which constitutes the ordinary line of action for impressions having their origin in the necessities of the Organic or Vegetative life of the individual. That the Will should have a certain degree of control over these movements, is necessary in order that they may be rendered subservient to various actions which are necessary for the due exercise of Man's psychical powers; but that they should not be left dependent upon its exercise, and should even be executed in opposition to it when the wants of the system imperatively demand their performance, constitutes a wise provision for securing Life against the chance of inattention or momentary caprice.

417. The Cerebro-Spinal system is intimately blended with another set of gangliionic centres and nerve-trunks, scattered in different parts of the body, but mutually connected with each other; this is commonly termed the *sympathetic* system; but not unfrequently, from the position of its principal centres, and their evident functional relation to the apparatus of Organic life, the *Visceral*

system. To this system we are probably to refer, not only the Semilunar and Cardiac ganglia (which seem to be its principal centres), with the chain of cranial, cervical, thoracic, lumbar, and sacral ganglia, which are in nearer connection with the Cerebro-spinal system; but also numerous minute ganglia,



which are to be found on its branches in various parts. Moreover, the ganglia upon the posterior roots of the Spinal nerves, and those upon the roots and trunks of certain Cranial nerves, may be ranked with considerable probability under the same category; and if such be the case, those fibres contained in the Cerebro-spinal nerves, which have these as their ganglionic centres, must also be accounted as belonging to the Sympathetic system. On the other hand, there unquestionably exist numerous fibres in the Visceral system, which proceed into it from the Cerebro-spinal system; these, however, are not uniformly distributed, for some of the Visceral nerves contain few or none of them, whilst in others they are numerous. The branches by which the Sympathetic system communicates with the Cerebro-spinal, and which were formerly considered as the *roots* of the Sympathetic system, seem to contain fibres of both kinds—*i.e.*, Cerebro-spinal fibres passing into the Sympathetic, and Sympathetic fibres passing into the Cerebro-spinal. The latter are chiefly, if not entirely, transmitted into the *anterior* branches of the Spinal nerves; the *posterior* branches being apparently supplied with sympathetic fibres from the ganglia on their own posterior roots. Some of these last fibres also pass from the Cerebro-spinal into the Sympathetic system. By these communications, the two systems of fibres are so blended with each other, that it is impossible to isolate them.—The branches proceeding from the Semilunar ganglia are distributed upon the vessels of the abdominal viscera; and those of the Cardiac ganglia upon the heart and vessels proceeding from it. The latter seem to accompany the arterial trunks through their whole course, ramifying minutely upon their surface; and it can scarcely be doubted that they exercise an important influence over their functions. What the nature of that influence may be, however, will be a subject for future inquiry (CHAP. XVII.). It is so evidently connected with the operations of nutrition, secretion, &c., that the designation 'Nervous system of organic life,' as applied to this system, does not seem objectionable, provided that we do not understand it as denoting

the *dependence* of these functions upon it.—The inter-penetration of the Cerebro-spinal system by the Sympathetic is strongly marked by these two circumstances;—that, in some of the lower Vertebrata, the distribution of their trunks cannot be separately distinguished; and that, even in the highest, some of the Glands, of which the secretion is most directly influenced by the condition of the mind, are supplied with most of their nerves from the cerebro-spinal system, the lachrymal and sublingual glands receiving large branches from the fifth pair, and the mammary glands from the intercostal nerves.

418. *Cerebro-Spinal Nerve-Trunks.*—Having thus considered the principal attributes of the ganglionic centres of the Cerebro-Spinal system, we have next to inquire into those of the nerve-trunks which are connected with them. The merit of the discovery of the difference between the *afferent* and *efferent* fibres of the nerves is almost entirely due to Sir C. Bell, who was led to it by a chain of reasoning of a highly philosophical character before any other physiologist came into the field.* Although his first experiments on the Spinal nerves were not satisfactory, he virtually determined the respective functions of their two roots—the posterior as *sensory* (afferent), the anterior *motor* (efferent) —by experiments, and by pathological observations upon the Cranial nerves, some of which contain only one class of fibres to the exclusion of the other. Subsequently his general views were confirmed by the very decided experiments of Müller; but until very recently, some obscurity hung over a portion of the phenomena. It was from the first maintained by Magendie, and has been subsequently asserted by other physiologists, that the posterior and anterior roots of the nerves were *both* concerned in the reception of impressions and in the production of motions; for that, on touching the posterior roots, not only the sensibility of the animal seemed to be affected, but muscular contractions were excited: and that, when the anterior roots were touched, the animal gave signs of pain, at the same time that convulsive movements were performed. These physiologists were not willing, therefore, to admit more than that the posterior roots were *especially* sensory, and the anterior *especially* motor. But the knowledge we now possess of the 'reflex' function of the Spinal Cord enables the former portion of these phenomena to be easily explained. The motions excited by irritating the posterior roots are found to be entirely dependent upon their connection with the Spinal Cord, and upon the integrity of the anterior roots and of the trunks into which they enter; whilst they are not checked by the separation of the posterior roots from the peripheral portion of the trunk; it is evident, therefore, that excitation of the posterior roots does not act immediately upon the muscles, through the trunk of the nerve which they contribute to form; but that it excites a reflex motor impulse in the Spinal Cord, which is propagated through the anterior roots to the periphery of the system.—The converse phenomenon of the apparent sensibility of the anterior roots of the Spinal Nerves or recurrent sensibility, as it is termed, has been investigated by M. Brown-Séquard. If these roots be irritated, the animal usually gives signs of uneasiness; but if they be divided, and the cut ends nearest the centre be irritated, none such are exhibited: whilst they are still shown when the farther ends are irritated, but not if the posterior roots are divided. M. Brown-Séquard† attributes these phenomena to cramp of the muscles supplied by anterior roots, the pain resulting from the violent compression of the extremities of the sensory nerves, which of course is no longer felt when the roots of the latter are divided. Others, however, finding

* See "British and Foreign Med. Review," vol. ix. p. 140, &c.

† "Lectures on the Physiology of the Central Nervous System," 1860; Lecture i.

that signs of pain are still given when the trunk of the mixed nerve is divided, consider that fibres of the posterior root, after descending a short distance, really turn back and enter the anterior root.

419. Every fibre, there is reason to believe, runs a distinct course, between the central organ, with one of the cells of which it is connected at one extremity, and the organ of sense, muscle, or other tissue, in which it either terminates or forms a loop at the other; in the terminal ramifications of the nerves, however, a *subdivision* and plexiform arrangement of the fibres is frequently observable. Although the fasciculi occasionally intermix and exchange fibres with one another (as occurs in a *plexus*), the fibres themselves never inosculate. Each fibre would seem, therefore, to have its appropriate office, which it cannot share with another.—Several objects appear to be attained by the plexiform arrangement. In some instances it serves to intermix fibres, which have endowments fundamentally different; for example, the Spinal Accessory nerve, at its origin, appears to be exclusively motor, and the roots of the Pneumogastric to be exclusively afferent; but by the early admixture of these a large number of motor fibres are imparted to the Pneumogastric, and are distributed in variable proportion, with its different branches; whilst a few of its sensory filaments seem to enter the Spinal Accessory.—In other instances, the object of a plexus appears to be to give a more advantageous distribution to fibres, which all possess corresponding endowments. Thus the Brachial plexus mixes together the fibres arising from five segments of the spinal cord, and sends off five principal trunks to supply the arm. Now if each of these trunks had arisen by itself, from a distinct segment of the spinal cord, so that the parts on which it is distributed had only a single connection with the nervous centres, they would have been much more liable to paralysis than at present. By means of the plexus, every part is supplied with fibres arising from several segments of the spinal cord; and the functions of the whole must therefore be suspended, before complete paralysis of any part can occur from a cause which operates above the plexus. Such a view is borne out by direct experiment; for it has been ascertained by Panizza that, in Frogs, whose Crural plexus is much less complicated than that of Mammalia, section of the roots of one of the three nerves which enter into it produces little effect on the general movements of the limb; and that, even when two are divided, there is no paralysis of any of its actions, all being weakened in a nearly similar degree.* All consideration of the mode in which we make use of our muscles, and of the power which we have over them, leads to the conclusion that each ganglionic centre has a specific and limited sphere of influence, producing certain movements and no others; hence, for the execution of a variety of movements in harmonious combination with each other, it seems requisite that the nervous supply of each muscle should be derived from several different centres; and thus it is, that the complication of plexuses comes to be related to the variety of movements of the parts supplied through them. It is not a little interesting to remark, that arrangements of a similar kind present themselves among the higher Invertebrata.

420. The following statements, in which the doctrines held by Müller† are adopted with some modifications and additions, embody the general principles ascertained by experiment, respecting the transmission of Sensory and Motor

* Striking illustrations of the importance of the plexiform communication of nerves are afforded by such cases as that recorded by Mr. Savory ("Lancet," Aug. 1, 1868), where, after excision of a portion of the musculo-spiral nerve, the sensibility of the parts supplied by it, though impaired, was still to some extent retained, in consequence probably of the communications that exist between the radial and external cutaneous nerves in the forearm. See also W. Gull, 'Gulstonian Lectures on the Nervous System,' in "Medical Times," 1849, p. 372.

† "Elements of Physiology," translated by Dr. Baly; pp. 680, 686.

impressions along the nerves which respectively minister to them. Their *rationale* will be at once understood, from the facts already mentioned in regard to the isolated character of each fibril, and the identity of its endowments through its whole course.

I. When the whole trunk of a *sensory* nerve is irritated, a sensation is produced, which is referred by the mind to the parts to which its branches are ultimately distributed; and if only part of the trunk be irritated, the sensation will be referred to those parts only which are supplied by the fibrils it contains.—This is evidently caused by the production of a change in the sensorium, corresponding with that which would have been transmitted from the peripheral organs of the nerves, had the impression been made upon them. Such a change only requires the integrity of the afferent trunk between the point irritated and the sensorium, and is not at all dependent upon the state of the peripheral part to which the sensations are referred; for this may have been paralysed by the division or other lesion of the nerve, or may have been altogether separated as in amputation, or the relative position of its parts may have been changed, as in autoplastic operations. So, when different parts of the thickness of the same trunk are separately and successively irritated, the sensations are successively referred to the several parts supplied by these divisions. This may be easily shown by compressing the ulnar nerve in different directions, where it passes at the inner side of the elbow-joint.—Still the mind undoubtedly does possess a certain power of discriminating the part of the nerve-trunk on which the impression is made; for whilst this impression is such as to produce sensations that are referred to its peripheral extremities, pain is at the same time felt in the spot itself; and it would seem as if slight impressions are *only* felt in the latter situation, at least in the normal condition of the trunk or fibre. Thus, as it has been well remarked by Volkmann, "if a needle's point be drawn in a straight line across the back, or the thigh, or any part in which the nerves are widely placed, the mind perceives the line of irritation as a straight one; whereas, if it referred all impressions to the ends of irritated fibres, this mode of irritation should be felt in sensations variously scattered about the line, at the points where the nerve-fibres crossed by the needle terminate."*

II. The sensation produced by irritation of a branch of the nerve is confined to the parts to which that branch is distributed, and does not affect the branches which come off from the nerve higher up.—The rationale of this law is at once intelligible; but it should be mentioned that there are certain conditions in which the irritation of a single nerve will give rise to sensations over a great extent of the body. This 'radiation of sensations' seems rather due, however, to a particular state of the *central* organs, than to any direct communication among the peripheral fibres.

III. In general the *motor* influence is propagated only in a centrifugal direction, and not in a retrograde course. It may originate in a spontaneous change in the central organs, or it may be excited in an impression conveyed to them through afferent nerves; but in both cases its law is the same. There is, however, a well-known experiment termed the "paradoxical contraction of muscle," which shows that motor-nerves may under certain circumstances convey impressions centripetally. If a motornerve be selected which divides into two branches (as for example the sciatic of the frog, which divides above the bend of the knee into the tibial and peroneal branches), and a galvanic stimulus be applied to either of these branches, this having been first divided above its insertion into the muscles, the electrotonic state will be

* Kirkes and Paget's "Handbook of Physiology," p. 375.

developed, not merely in the portion of the trunk continuous with that branch, but also in that which is continuous with the other branch, as will be made apparent by the contraction in the muscles supplied by the latter. That this experiment may be free from the possible fallacy resulting from the excitement of reflex action, the trunk of the sciatic nerve should be divided high up, or the spinal cord be destroyed.—Lastly, the occurrence of the negative oscillation of the current, that is to say, the disappearance of the normal current which exists in both sensory and motor nerves, on stimulation of these nerves by any stimulus, affords an additional proof that the particles of nerves can conduct in either direction. In the same way, although as a rule sensory impressions are only conducted towards the new centres, yet some evidence has been obtained to show that they may conduct in an opposite direction. Thus, MM. Philippeaux and Vulpian* divided the hypoglossal and lingual nerves, which are conveniently placed for the experiment, and applied the peripheric extremity of the hypoglossal to the centric extremity of the lingualis. They found that in a few weeks union took place, and that the muscles of the tongue might be excited to contract by an electrical current applied to the lingualis or sensory nerve. MM. Philippeaux and Vulpian drew the conclusion that when the properties of the hypoglossal are abolished by section the lingualis after the lapse of some time acquires motor fibres it did not previously possess. It is to be observed, however, that although the fibres can thus conduct an electrical stimulus there is total loss of *voluntary* control over the lingual muscles, and if the operation be performed on both sides the animal is rendered permanently incapable of protruding its tongue. In Bidder's experiments,† microscopical examination of the nerves showed that the peripheric extremity of the lingualis consisted exclusively of nerve-fibres which had undergone fatty degeneration, whilst in the peripheric portion of the hypoglossal which had united with the centric of the lingualis, the greater number of the fibres presented their normal characters. And this accorded with the fact that, when the nerve was cut during life, the animal gave marked indication of pain, and the same side of the tongue was convulsed.

IV. When the whole trunk of a motor nerve is irritated, all the muscles which it supplies are caused to contract. This contraction evidently results from the similarity between the effect of an artificial stimulus applied to the trunk in its course, and that of the change in the central organs by which the motor influence is ordinarily propagated. But when only a part of the trunk or a branch is irritated, the contraction is usually confined to the muscles which receive their nervous fibres from it; in this instance, as in the other, there is no lateral communication between the fibrils.

421. *Determination of the Functions of Nerves.*—Various methods of determining the functions of particular nerves present themselves to the Physiological inquirer. One source of evidence is drawn from their *peripheral distribution.* For example, if a nervous trunk is found to lose itself entirely in the substance of Muscles, it may be inferred to be chiefly, if not entirely, *motor* or *efferent.* In this manner Willis long ago determined that the Third, Fourth, Sixth, Portio Dura of the Seventh (or Facial), and Ninth cranial nerves, are almost entirely subservient to muscular movement; and the same had been observed of the fibres proceeding from the small root of the Fifth pair, before Sir C. Bell experimentally determined the double function of

* MM. Philippeaux and Vulpian, "Comptes Rendus," 1860, t. ii. p. 363, and idem, t. iii. p. 58. "Archiv. Gén. de Médecine," July, 1863, p. 122. See also Gluge and Thiernesse, Brown-Séquard's "Journal de la Physiologie," 1859, t. ii. p. 686.

† Reichert's "Archiv," 1865, p. 246.

that division of the nerve into which alone it enters. Again, where a nerve passes through the muscles, with little or no ramification among them, and proceeds to a Cutaneous or Mucous surface on which its branches are minutely distributed, there is equal reason to believe that it is of a *sensory* or rather of an *afferent* character. In this manner Willis came to the conclusion, that the Fifth pair of cranial nerves differs from those previously mentioned, in being partly sensory. Further, where a nerve is *entirely* distributed upon a surface adapted to receive impressions of a *special* kind, as the Schneiderian membrane, the retina, or the membrane lining the internal ear, it may be inferred that it is not capable of transmitting any other kind of impressions; for experiment has shown that the *special sensory* nerves do not possess common sensibility. The case is different, however, in regard to the sense of taste, which originates in impressions not far removed from those of ordinary touch; and it is probable that the same nerves minister to both.—Anatomical evidence of this kind is valuable also, not only in reference to the functions of a principal trunk, but even as to those of its several branches, which, in some instances, differ considerably. Thus, some of the branches of the Pneumogastric are especially motor, and others almost exclusively afferent; and anatomical examination, carefully prosecuted, not only assigns the reasons for these functions, when ascertained, but is in itself nearly sufficient to determine them. For the superior laryngeal branch is distributed almost entirely upon the mucous surface of the larynx, the only muscle it supplies being the crico-thyroid; whilst the inferior laryngeal or recurrent is almost exclusively distributed to the muscles. From this we might infer, that the former is an afferent, and the latter a motor nerve; and experimental inquiries (as we have seen, § 275, 276) fully confirm this view. In like manner it may be shown, that the Glosso-pharyngeal is chiefly an afferent nerve, since it is distributed to the *surface* of the tongue and pharynx, and scarcely at all to the muscles of those parts; whilst the pharyngeal branches of the Pneumogastric are chiefly, if not entirely, motor (§ 91). Lower down, however, the branches of the Glosso-pharyngeal cease, and the œsophageal branches of the Pneumogastric are distributed both to the mucous surface and to the muscles, from which it may be inferred that they are both afferent and motor; a deduction which experiment confirms.—We perceive, therefore, that much knowledge of the function of a nerve may be obtained from the attentive study of its ultimate distribution; but it is necessary that this should be very carefully ascertained, before it is made to serve as the foundation for physiological inferences. As an example of former errors in this respect, may be mentioned the description of the Portio dura of the Seventh (or Facial) at first given by Sir C. Bell; for he incorrectly stated it to be distributed to the skin as well as to the muscles of the face, and erroneously regarded it as in part an afferent nerve, subservient to respiratory impressions as well as to motions. In the same manner, from inaccurate observation of the ultimate distribution of the Superior Laryngeal nerve, it was long regarded as that which stimulated to action the constrictors of the glottis.

422. But the knowledge obtained by such anatomical examinations alone is of a very general kind; and requires to be made particular,—to be corrected and modified,—by other sources of information. One of those relates to the *connection of the trunks with the central organs.* The evidence derived from this source, however, is seldom of a very definite character; and, in fact, Physiologists have rather been accustomed to judge of the functions of particular divisions of the nervous centres by those of the nerves with which they are connected, than to draw aid from the former in the determination

of the latter. Still this kind of examination is not without its use, when there is reason to believe that a particular tract of fibrous structure has a certain function, and when the office of a nerve whose roots terminate in it is doubtful. Here again, however, very minute and accurate examination is necessary, before any sound physiological inferences can be drawn from facts of this description; and many instances might be adduced to show, that the real connections of nerves and nervous centres are often very different from their apparent ones.

423. Most important information as to the functions of particular nerves may be drawn from *experimental inquiries;* but these also are liable to give fallacious results, unless they are prosecuted with a full knowledge of all the precautions necessary to insure success. Some of these will be here explained.—In the first place, the endowments of the *trunk* and of the *roots* of a nerve may differ; owing to the admixture, in the former, of fibres derived by inosculation from another nerve (§ 420). Hence, in order to attain satisfactory results, a comparative set of experiments should always be made upon each.—A nerve-trunk may be too hastily considered as *motor* or efferent, on account of the excitation of muscular movements by irritation of its trunk, whilst still in connection with its centre; for such movements may be called forth, not only by the direct influence of the nerve upon the muscles, but also by reflex stimulation acting through the ganglionic centre upon some other nerve. The real nature of such movements can only be determined by dividing the trunk, and then irritating each of the cut extremities. If, upon irritating the end *separated* from the centre, secretion or muscular contraction be produced, it may be safely inferred that the nerve is, in part at least, of an *efferent* character. Should no such result follow, this would be improbable. If, on the other hand, muscular movement or secretion should be produced by irritating the extremity *in connection with* the centre, it will then be evident, that it is occasioned by an impression conveyed *towards* the centre by *this* trunk, and propagated to the muscles or glands by some other; in other words, to use the language of Dr. M. Hall, this nerve is an 'excitor' of motion, not a direct motor nerve. The Glosso-pharyngeal has been satisfactorily determined, by experiments of this kind, performed by Dr. J. Reid (§ 91), to be chiefly, if not entirely, an afferent nerve.—It has been from the want of a proper mode of experimenting, that the functions of the *posterior* roots of the Spinal nerves have been regarded as in any degree motor. If they be irritated, without division of either root, motions are often excited; but if they be divided, and their separated trunks be then irritated, no motions ensue; nor are any movements produced by irritation of the roots in connection with the spinal cord, if the *anterior* roots have been divided. Hence it appears that these fibres do not possess any direct motor powers, but that they convey impressions to the centre, which are reflected to the muscles through the anterior roots.—The same difficulties do not attend the determination of the *sensory* endowments of nerves. If, when the trunk of a nerve is pricked or pinched, the animal exhibits signs of pain, it may be concluded that the nerve is capable of receiving and transmitting sensory impressions from its peripheral extremity. But it not unfrequently happens that this capability is derived by inosculation with another nerve; as is the case with the Facial, which is sensory after it has passed through the parotid gland, having received there a twig from the Fifth pair.

424. The fallacies to which all experiments upon the nerves are subject, arising from the partial loss of their power of receiving and conveying impressions, and of exciting the muscles to action, after death, are too obvious to require more particular mention here; yet they are frequently overlooked.

Of a similar description are those arising from severe disturbance of the system, in consequence of operations; which also have not been enough regarded by experimenters.—As a general rule, *negative* results are of less value than *positive*, but very careful discrimination is often required to determine what *are* negative, and what positive results. Each particular case has its own sources of fallacy, which require to be logically scrutinized; and the only satisfactory proof is derived from the concurrence of every kind of evidence which the nature of the inquiry admits of. Thus in the determination of the functions of a particular nerve-trunk, it should be shown that a certain effect is *constantly* produced by its excitation (under the conditions laid down in the preceding paragraph), and that a corresponding interruption in the action to which it is hence inferred to be subservient, takes place when its continuity has been interrupted: by this double proof, the Glosso-pharyngeal and the Pneumogastric are shown to be the principal, but not the sole, excitors of the movements of Deglutition and Inspiration respectively. But the evidence afforded solely by the interruption of a particular function, after the division of a certain nerve, or the destruction or removal of a nervous centre, is by no means so satisfactory; for this may be occasioned rather by the general effects of the operation, than by the simple lesion of the nervous apparatus. In order to get rid, so far as possible, of this source of fallacy (which particularly affects experiments upon the Encephalic centres, and upon the influence of the nerves upon the viscera), it is desirable to perform comparative experiments, in which the general injury shall be as nearly as possible the same, and the only difference shall lie in the lesion of the nervous system; and to subtract from the entire result all that can be thus shown to be attributable to the general disturbance produced by the operation. But even then, it may happen that the function is only suspended for a time, by the shock which has been induced by the injury to the nerve; and if it should be subsequently renewed without any reunion of the trunk, we have the most convincing proof that whatever degree of participation the nerve may have in it, the action is not essentially dependent upon the integrity of that portion of the nervous apparatus. Such we have seen to be the case in regard to the relation of the Pneumogastric nerves to the secretion of gastric fluid in the walls of the stomach (§ 118).

425. All our positive knowledge of the functions of the Nervous System in general, save that which results from our own consciousness of what passes within ourselves, and that which we obtain from watching the manifestations of disease in Man, is derived from observation of the phenomena exhibited by animals made the subjects of experiments; and in the interpretation of these, great caution must be exercised.—In the first place it must be constantly borne in mind that, except through the *movements* consequent upon them, we have no means of ascertaining whether or not particular changes in the Nervous System, whose character we are endeavouring to determine, are attended with sensation; since we have no power of judging whether or not this has been excited, save by the cries and struggles of the animal made the subject of experiment. Now although such cries and struggles are ordinarily considered as indications of pain, yet it is not right so to regard them in every instance; and the only unequivocal evidence is derived from observation of the corresponding phenomena in the Human subject; since we can there ascertain, by the direct testimony of the individual affected, what impressions produce sensation, and what excite movements independently of sensation. Further, we are not justified in assuming that Consciousness is excited by an irritation, still less that Intelligence and Will are called into exercise by it, merely because movements evidently tending to get rid of its source are performed in correspon-

dence to it. We know that the contractions of the heart and alimentary tube are ordinarily excited by a stimulus, without any sensation being involved; and these movements, like all that are concerned in the maintenance of the Organic functions, have an obvious *design*, when considered either in their immediate effects, or in their more remote consequences. The character of *adaptiveness*, then, in Muscular movements excited by external stimuli, is no proof that they are performed in obedience to sensation; much less that they have a voluntary character. In no case is this adaptiveness more remarkable, than in some of those actions which are not only performed without any effort of the will, but which the will cannot imitate. This is the case, for example, with the act of Deglutition (§§ 89, 90), the muscles concerned in which cannot be thrown into contraction by a voluntary impulse, being stimulated only by impressions conveyed from the mucous surface of the fauces to the Medulla Oblongata, and thence reflected along the motor nerves. No one can swallow, without producing an impression of some kind upon this surface, to which the muscular movements will immediately respond. Now it is impossible to conceive any movements more perfectly adapted to a given purpose, than are those of the parts in question; and yet they are independent, not only of volition but of sensation, being still performed in cases in which consciousness is completely suspended or entirely absent. The act of Sucking in the infant, again, is one in which a number of muscles are called into combined contraction, in a manner which shows a complete adaptation to a given purpose; and yet it is impossible to suppose this adaptation to be *purposive* on the part of the infant itself; more especially as it is shown both by the occurrence of monstrosities, and by experiments made with this object, that no part of the Cranio-spinal axis above the Medulla Oblongata is necessary to it. And in the acts of Coughing and Sneezing (§ 280), we have additional examples of the most *adaptive* movements, executed by a marvellous combination of separate muscular actions, with the obvious purpose of removing sources of irritation from the air-passages; and yet we know by personal experience that this combination is *not* made with any design of our own.

426. The activity of the nervous ganglia and of the nervous cords is alike called into action by the application of *stimuli*. These vary in their nature, and whilst some, as electrical currents, chemical agents, and mechanical pressure, can excite all nerves to action, others, like the vibrations of light and sound, odorous emanations, and heat, appear to be only capable of exciting nerves whose intimate structure especially adapts them for responding to the impressions made by these delicate yet active agents. Although the conducting power of the Nerves for electrical currents is many thousand times less than metallic threads, electricity appears to be a stimulus that very readily affects them, whatever may be their function; exciting not only the various sensory nerves, but being also the most powerful agent with which we are acquainted for inducing the contraction of muscles when applied to the motor nerves that supply them. The effects of electricity upon nerves differ remarkably according to whether a continuous or an induced current is employed. A continuous current passed across a nerve at right angles occasions very slight if any contraction in the muscle supplied by it;* but if it be directed up or down the nerve, contraction commonly occurs at the moment of closing and opening the current, though there is none during its steady and uniform passage.† With an induced or interrupted current, on the contrary, the nerve being kept in a constant state of excitation, the muscles supplied by it pass into a state of

* See Albrecht, Meyer and Giuffré, Pflüger's "Archiv," 1880, Band xxi. p. 462.

† The effects of different kinds of stimulation on various nerves has been studied by Grützner, Pflüger's "Archiv," Band xvii. p. 215.

permanent or tetanic contraction. With a continuous current, contraction is observed to take place not only at the moment of closing and opening, but also when any sudden change, either of increase or decrease, occurs in the intensity of the transmitted current. There is, moreover, a certain strength of current which causes the muscle to pass into a state of Tetanus, 'named galvano-tetanus,' or 'galvano-tonus.' The observation of these phenomena has led to the establishment of a law of nerve physiology, which was originally laid down by Du Bois-Reymond, that the excitation of a nerve is effected not so much by the absolute amount or intensity of the stimulus that is applied to it, as by the modification of this amount from one moment to another. In other words, the excitation of any nerve caused by a stimulus is greater the more rapidly the resulting changes are produced, or the greater they are in a given time; and on the contrary, whatever may be the nature of the stimulus applied, whether mechanical, chemical, thermic, or electrical, neither sensation in a sensory nerve, nor motion in a motor nerve is produced when the passage from one grade of intensity to another is extremely gentle. If, for example, mechanical pressure be so applied to a *motor* nerve as that commencing with the slightest possible contact it may steadily and continuously increase in force even till the nerve be killed at that spot, no convulsions occur in the muscles to which the nerve is distributed.* Muscular contraction only supervenes where the change in the amount of pressure, whether greater or less than that previously present, is so sudden as to produce a kind of shock. In proportion to the energy of the shock or vibration of the particles of the nerve is the effect produced on the muscles. Heidenhain† has constructed an instrument which he has named a "mechanical tetanomotor" which shows that the mechanical stimulus required to excite a nerve is by no means inappreciable. By this instrument it may be demonstrated that a blow so slight as to fail to cause contraction of the muscle supplied by the nerve augments the excitability of the nerve to a subsequently applied stimulus, whilst a somewhat stronger blow diminishes the excitability and conductivity of the nerve at the point struck, and if the blow be violent, both excitability and conductivity are lost at the point struck.‡ The excitability of a nerve is sometimes increased by slight extension,§ whilst violent extension induces tetanic convulsions in the muscles supplied by the stretched nerve. The whole body of a decapitated Frog can sometimes be rendered rigid by throwing it on the ground. In a similar manner, whilst the sudden application of a ligature or of heat to a *sensory* nerve produces acute pain, numbness passing into entire insensibility is the only effect if either be gradually applied,‖ and the same holds good for all other kinds of stimuli. In all instances the passage of a nerve from a state of rest to one of functional activity is accompanied by changes in the chemical constitution of the tissue, and it has been shown that whilst the substance of the brain, spinal cord, and nerves is feebly alkaline or neutral when at rest, it becomes distinctly acid after long and exhausting activity.¶ The molecular and chemical changes seem to be more readily induced in sensory than in motor nerves, the latter requiring more powerful stimulation to call them into play than the former, their equilibrium in other words being more stable. Chauveau** has endeavoured to explain the effects of *electrical currents* on the supposition that

* Schiff, "Physiologie," 1839, p. 94.

† Moleschott's "Untersuchungen," Band iv. 1858, p. 124.

‡ See Wundt, "Untersuch. zur Mechanik. der Nerven," Band i. 1871, p. 198.

§ See Schleich, "Zeits. f. Biologie," Band vii. 1871, p. 391.

‖ See Heinzmann, 'Uber die Wirkung sehr allmähliger Aenderungen thermische Reize auf die Empfindungsnerven,' Pflüger's "Archiv," Band vi. p. 222.

¶ By Funke, Gscheidlen, and Ranke, "Centralblatt," 1869, p. 97.

** Chauveau, Brown-Séquard's "Journ. de la Physiologie," 1859, p. 576.

they produce a mechanical commotion in the particles of the nerve. Hence induced currents, which are currents of high tension, and therefore produce a more powerful shock or series of shocks, constitute stronger stimuli than continuous currents, in which the quantity of electricity is large.* On applying a continuous current to a nerve contraction takes place in the muscle it supplies, and a similar contraction occurs at the moment when the current is broken, because at these periods, in accordance with Du Bois-Reymond's law, there is a sudden change in the molecular constitution of the nerve. When the interruptions of a continuous current are about twenty in the second, the muscle has not time to relax between the periods of breaking and making contact and passes into a state of tetanus. The induced currents which are developed in a secondary coil on closing and opening the current in a primary coil, as in the instruments of ordinary construction, are always of short duration, and the molecular movement produced in the nerve is correspondingly rapid and sudden. The duration of the opening does not exceed 0″·0042, whilst the duration of the closing current is 0″·0114. The closing current is comparatively weak, its proportion to the opening current being as 1 : 6, the latter being of higher tension and of shorter duration. Chemical stimuli act but slowly on nerves as compared with their action on muscles, which we may attribute to the sheath of the fibres affording a certain amount of protection to the contents, and thus allowing them to be only gradually acted on. The sensory nerves appear to be much more readily acted on, and by a much greater range of *chemical agents*, than the motor nerves; powerful stimuli for the latter are, however, found in solutions of Soda and Potash, even when not exceeding one tenth per cent., in those of Nitrate of Potash and of Hydrochloric acid, containing 20 per cent., and in concentrated solutions of Ammonia and Alcohol (90 per cent.); the latter, however, rapidly killing the nerve at the point where they have been applied. Bisulphide of carbon, the ethereal oils, and concentrated mineral acids kill the nerve at once, without producing convulsions.† Distilled water applied to nerve-trunks excites no muscular contractions, but if injected into the vessels distributed to a muscle induces very violent convulsions, which are believed by Schiff to be due to the direct effect of the water upon the delicate terminations of the nerves in the muscles. Withdrawal of water from the nerves, if performed either gradually, or with extreme rapidity, produces no effect, but if accomplished with moderate rapidity causes tetanus.‡ The longer the portion of nerve exposed to desiccation, the more violent is the tetanus. The contractions of the muscle begin when the nerve has lost about 4 per cent. of its weight, and its excitability is lost when about 20 per cent. has evaporated.§ The sudden deprivation of water from the nerves may perhaps account in part at least for the spasms of cholera. If too large an amount of water have not been withdrawn, the function of the nerve may be restored on again moistening it. The nerves of frogs, which naturally contain 76·3 per cent. of water, will imbibe a larger quantity till they contain 93·2 per cent. As regards *thermic irritation* as a stimulus for the nerves, it has been shown by Weber that the sensory nerves do not perceive positive temperature, but only variations in the degree of heat of external objects. The influence of variations of temperature on motor nerves has been investigated by Eckhard, who has shown that a temperature of about 130° F.

* For an account of the action of induced and continuous currents on healthy and on paralysed nerve and muscle respectively, see Onimus, Robin's "Journal de l'Anatomie," 1874, translated in full in the "Practitioner," 1874–75.

† Schiff, "Physiologie," 1859, p. 101.

‡ Harless, "Zeitschrift f. rat. Med.," Band vii. 1859, p. 219.

§ Birkner, "Das Wasser der Nerven," &c., 1868; and Rauke, "Die Lebensbedingungen der Nerven," 1868.

produces convulsions in frogs, which, however, soon cease; the irritability of the nerves being then lost, though upon cooling they occasionally regain it. Sudden exposure to a temperature of about 25° F. also produces convulsions.* Temperatures intermediate to these limits do not occasion convulsions, but the nerve soon loses its irritability permanently when exposed to a temperature approximating either the higher or the lower extreme.

427. During life, and in the healthy state, the excitability of a motor nerve gradually diminishes from its origin to its distribution in the muscle, so that a stimulus of determinate intensity produces a more energetic contraction of a muscle in proportion to the distance from the muscle that it is applied to the nerve, or, as it is expressed by Pflüger, in proportion to the length of the myopolar portion of nerve. Thus Budge found that to produce the same effect—*i.e.*, the same amount of contraction—it was necessary to apply a stimulus of more than double the strength close to a muscle, than was requisite if the stimulus were applied to the portion of nerve near its origin. The question arises whether the nerve is itself more excitable at the parts nearer the centre, or whether the stimulus does not gain force in its descent, and produce, like an avalanche, an effect greater in proportion to the distance it has traversed. Pflüger expresses himself decisively in favour of the latter supposition. Yet it seems opposed to our ordinary notions of the resistance offered to the passage of currents by conductors, and the phenomenon appears to be more readily explicable on the supposition that the structure of the nerve, and especially of its sheath, may be more delicate in those parts which are more protected, and that it consequently more readily responds there to impressions. Nerves seem to react equally throughout their whole length to chemical stimuli. After death the excitability of the nerves dies out centrifugally, the part in proximity to the muscles remaining longest excitable; immediately after death the excitability of the nerve is for a short period considerably exalted, and this exaltation is shorter in duration in proportion to the distance of the portion of nerve examined from the muscle. If a nerve be divided it becomes temporarily more excitable from the centre towards the periphery, but after a time it ceases to be excitable. This process takes place more rapidly in the proximal than in the peripheral portion of the divided nerve, and the fact is known as the "Law of Ritter-Valli." According to Oehl,† if the needle of a sensitive thermo-electric apparatus be made to traverse a large nerve like the sciatic, a marked increase of temperature occurs at the moment that its functional activity is excited by mechanical or electrical excitation; both Heidenhain and Helmholtz have, however, failed to corroborate this assertion.

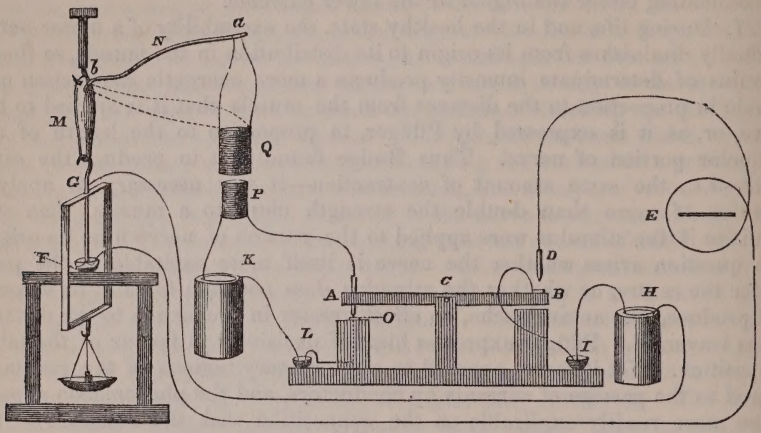
428. The ingenuity of Helmholtz has enabled him to ascertain with some precision the rate at which the change induced by the passage of an electrical current is propagated along a small portion of a nerve. The following figure and description deserve attention, since they exhibit the mode in which physical research can be applied to the most recondite questions of animal life. It is required to measure the time which any excitation takes to travel from the cut end *a* of the nerve N to its point of entrance *b* into the muscle M. As the means of excitation, Helmholtz employs an instantaneous induction current in the following mode:—At the moment that a constant current passing through the coil P, from the

* Eckhard, "Zeitschrift f. rat. Med.," Band x. p. 165; and Harless, ibid., Band viii. p. 122.

† "Annali Universali," tom. cxc. 1864, p. 465; 1865, p. 601; and Lombard, "Med.-Chir. Rev.," Jan. 1869.

battery K, *is broken*, an instantaneous *induced* current passing in the same direction is excited in Q; this is the stimulus acting on the nerve at *a*. The time-measuring current is formed by a second battery H, into some part of whose circuit a galvanometer E is introduced. It is requisite that the

FIG. 196.



closure of this current should be precisely coincident with the opening of the inducing current from K, by which the induced current at Q, or the stimulus, is produced; this is effected by the lever A B C, whose arm A rests on the metal plate O and completes the circuit K L A P. If now the metal point D be forcibly pressed on B, the time-measuring current passing through H I B D E F G will be closed; but at the same instant, from the depression of the arm B, the stimulus will be applied to the nerve through the opening of the inducing current K L A P, which is the result of the elevation of the arm A. But as soon as the stimulus has reached the muscle M, after traversing the nerve N the muscle contracts, raising with it the hook G, which just dips into the cup of mercury F, and consequently breaking the time-measuring current proceeding from the battery H. The *extent* to which the galvanometer needle has been deflected indicates the time during which the current has been flowing through the circuit H I B D E F G, that is, the time which has intervened from the instant of the application of the stimulus to the nerve at *a*, to the moment when the contraction of the muscle breaks that current. A portion of this time is occupied in the transmission of the stimulus from the point *a* to the muscle, and a portion, termed the period of latent excitation, elapses before the muscle responds to the stimulus. In order to ascertain the duration of the former period, the experiment is repeated with this alteration, that the stimulus is applied at *b*, and again the extent to which the needle is deflected is read off; the difference between the two observations then gives the time occupied by the stimulus in passing from *a* to *b*. From numerous experiments with this instrument, Helmholtz arrived at the conclusion that in the Frog, at a temperature between 52° F. and 70° F., the rapidity of the propagation of impressions along motor nerves was from 81 to 126 feet per second, and he estimates the rapidity for human nerve at somewhat more than 200 feet per second.* Other observers

* According to Troitzky, with feeble currents the maximum velocity of propagation is between 50° and 68° Fahr., the rapidity being greatly reduced when the nerve (in the Frog) is warmed to 86° or cooled to 0° Fahr. With strong currents the influence of the temperature upon the conductivity of the nerves diminishes or becomes altogether imperceptible

have obtained the following results:—Hirsch,* 34 meters (111·5 feet); and Schelske,† 29·6 meters (98·4 feet) per second in the Frog. Marey,‡ from 12 to 15 meters (36 to 48 feet) per second in the same animal in winter. Donders and de Jaager, § 26·09 meters (88 feet) for the sensory nerves of Man. And Kohlrausch‖ also from experiments on Man, at 94 meters (308·3 feet) per second. Still more recently Helmholtz,¶ in experiments conducted with Herr Baxt, obtained the number 33·905 m. (111·22 feet) for Man, whilst Place and van West** found that the mean velocity in man was 53 meters (174 feet) per second. In these experiments, as well as in those of Munk, it was found that the rapidity of transmission is greater in the *peripheral* than in the more centrally situated portions of the nervous system. Colin†† has noticed that if the sympathetic ganglia are strongly irritated, reflex movements are immediately produced; but when the excitation is more feeble, a longer time elapses before the movements occur. M. Hirsch has even attempted to determine the relative rapidity with which impressions are transmitted through the nerves of sight, hearing and touch; and the following Table gives his conclusions, in which the term 'Physiological time' signifies the period occupied in the perception of the impression, and in the origination of the motor impulse and execution of the muscular movement by which the time was registered:—

Sense.	Hirsch.		Hankel.‡‡
	Physiological Time.	Mean Variation.	Physiological Time.
1. Hearing	0·149	± 0·025	0·1505
2. Visual perception of a spark	0·200	± 0·016	0·2057
3. Visual perception of the transit of a star	0·077	± 0·025	
4. Touch (left hand)	0·182	± 0·016	0·1546

Thus it will be observed that the perception and registration of an unexpected appearance (spark) occupies much more time than the perception of a slowly-awaited one (transit observation), and one-third more than even the perception of a sound; but the mean variation in the latter case is considerably greater. The value of such experiments in affording information respecting the rapidity of conduction of sensory nerves is, however, but small, since the total or physiological time occupied includes: 1. The time required for the reception of the sensation at the integument. 2. The time required for its transmission through the sensory nerve. 3. The conversion of the sensory impulse into a motor impulse. 4. The transmission of this impulse through the motor nerve, and lastly, the execution of the muscular contraction, each of which events may occupy a variable time.

429. *Electrical Phenomena in Nerve and Muscle.—Pre-existence Theory of Du Bois-Reymond.*—The electrical phenomena presented by the nerves and muscles are in many respects so similar that it will prevent repetition if they

(Pflüger's "Archiv," Band viii. Heft xii.). Both these experiments and the antecedent ones of Helmholtz and Baxt ("Monatsbericht d. Berlin Acad.," 1870, p. 184) show that the influence of temperature must not be overlooked in examining the conductivity of nerves.

* Moleschott's "Untersuch.," Band ix. 1863, p. 183. † Reichert's "Archiv," 1864, p. 151.

‡ "Gaz. Méd. de Paris," 1866, p. 124. § "Nederlandsch. Archief," Band i. p. 518.

‖ Henle, Pfeuffer's "Zeits.," Band xxviii. 1866, p. 190.

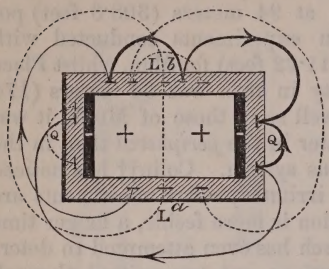
¶ "Berichte der Berliner Akadem.," 1867, p. 229.

** Pflüger's "Archiv," Band iii. p. 424. †† "Comptes Rendus," 1861, tom. i. p. 969.

‡‡ "Ber. d. k. Sachs. Gesell. der Wiss.," Feb. 1866.

are here considered together.* When a small piece of a nerve-trunk or a cylindrical or fusiform muscle is cut out from the recently-killed body, and is so placed upon the electrodes of a Galvanometer that it touches one of them with its surface (or natural *longitudinal* section), and the other with its cut extremity (or artificial *transverse* section), a considerable deflection of the index is produced, the direction of which always indicates the passage of a current—the natural nerve current—from the interior to the exterior of the nerve-trunk, or from the longitudinal section through the galvanometer to the transverse section. This is shown diagrammatically in Fig. 197. It is indifferent in regard to the direction of the current, whether the central or the peripheral cut extremity be applied to the electrode; and, in fact, the most powerful effect is obtained by doubling the nerve in the middle, and applying both tranverse sections to one electrode, whilst the loop is applied to the other. On the other hand, if the electrodes be applied to the two cut extremities no decided effect is produced; and the same neutrality exists between any two points of the surface of the trunk, equidistant from the middle of its length or equator (*a b*, Fig. 197); but if the points be not equidistant, then a deflection is produced, indicating that the parts nearer the middle are positive to those nearer the extremities. It has not been found possible, owing to the small size of the nerve-trunks experimented on, to test in a similar manner the relative state of different points of their transverse section; but there can be little doubt, from the complete conformity which exists in other respects between nervous and muscular currents, that the same law will be found to prevail in the former as in the latter case—namely, that the points nearer the surface are positive to those nearer the centre. There is no difference between the motor and the sensory nerves in regard to the direction of this current, the existence of which Du Bois-Reymond believed he could demonstrate not only by the galvanometer, but also by the excitement of contractions in the limb of a galvanoscopic frog. Its strength in the Frog he found amounted to 0·022 Daniell, and in the Rabbit to 0·026.—The 'nervous current,' like the muscular, must, he considered, be derived from the electro-motive action of the molecules of the nerve; every integral particle of the nervous substance becoming a centre of electro-motor action, and containing within itself positive and negative elements. It is indifferent what form is assigned to these electro-motive molecules; but it would seem that they must have two negative polar zones, and a positive equatorial zone; a combination of such elements being able to produce all the electrical effects of a nerve in a state of rest. It seems altogether best to suit the phenomena, to suppose that each of these *peripolar*

Fig. 197.



This figure is intended to show the direction of the currents in a columnar portion of nerve or muscle. L, longitudinal section; Q, Transverse section; *a*, *b*, the equator. The barbed lines indicate the direction, and their thickness the force of the currents established, when the electrodes of a galvanometer are applied to the corresponding surfaces. The dotted lines show inoperative arrangements.

* The principal works to be consulted on this subject are Du Bois-Reymond, "Untersuchungen über thierische Electricität," in which a complete list of all previous works is contained. Wundt, "Untersuchungen zur mechanik der Nerven und Nerven centren," 1871. Munk, Hermann, Pflüger, and others in Pflüger's "Archiv f. gesammte Physiologie," 1868–1880. Onimus, "Archives de Physiologie," 1874, and Hermann in the "Handbuch der Physiologie," 1879.

molecules is formed by the combination of two *dipolar* molecules, touching each other by their positive poles,—as in the subjoined Table, which represents a band of four series, A, B, C, D, each series containing four dipolar molecules :—

	1.	2.	3.	4.
A	−+ +−	−+ +−	−+ +−	−+ +−
B	−+ +−	−+ +−	−+ +−	−+ +−
C	−+ +−	−+ +−	−+ +−	−+ +−
D	−+ +−	−+ +−	−+ +−	−+ +−

The relative position of these sets of molecules may, however, under certain circumstances, be changed; and the very remarkable modification of the 'nervous current,' which has been shown by M. du Bois-Reymond to follow severe injuries of the nerve by mechanical, chemical, or thermal agencies, appears to be attributable to such an alteration. If, for instance, a piece of hot metal be brought near to the nerve without touching it, the nervous current will be seen to diminish rapidly, and to have its direction reversed, during which the property possessed by the nerve of conveying irritation to the muscle, though impaired, is not destroyed; and if, whilst in this abnormal state, the nerve be divided, every transverse section is found neutral or positive to the longitudinal section, instead of negative. If the nerve-trunk be then placed between muscles, so as to recover its natural moisture, it will at the same time recover its usual electro-motive power. The same phenomenon is often exhibited in winter, when the frogs serving for experiment have been exposed to cold. The muscle or nerve is then said to present a 'parelectronomic' behaviour, which Du Bois-Reymond explained by assuming that in the case of muscle there is a layer of muscle in contact with the tendon which acts electro-motorially in an opposite direction, and this equals, or even over-compensates, the normal current. To represent this parelectronomic layer, it is only requisite to take away the ultimate molecule of the dipolar molecule, when the last one will turn its positive side to the surface. According to M. du Bois-Reymond, the *current* shown by the entire nerve, when made to form part of a circuit, is only a *derived* current produced by incomparably more intense currents circulating in the interior of the nerve around these ultimate particles, varying greatly in intensity according to the mode in which these particles are arranged; but, generally speaking, increasing both with the length and with the thickness of the nerve.

430. *Alteration Theory of Hermann.*—Hermann is at issue with Du Bois-Reymond on several points. He contends* that in perfectly uninjured animals the nerves and muscles, when at rest, are absolutely destitute of any current, and that all currents that can be made manifest are due to injury inflicted on the tissue, leading to more rapid oxidation at the point injured, followed by death. This part, which extends in the nerves as far as the first constriction ring of Ranvier, then becomes negative to the remainder of the nerve; but if a new section be made, the presence of a current, as Engelmann has shown, can again be made manifest. But supposing a muscle to exhibit a well-marked current, it will be found that on throwing it into a state of tetanic contraction by interrupted electrical stimulation of its nerve, the current undoubtedly diminishes and a negative variation occurs, as stated by Du Bois-Reymond. In the case of a *nerve* a similar wave, which Hermann prefers to term an 'action current,' propagates itself from the point of stimulation in both directions, centripetally as well as peripherically, or if a series of shocks be applied,

* Hermann, "Handbuch du Physiologie," Band i. 1879, p. 169.

a series of such waves is produced. The duration of the action current does not exceed 1·1430th of a second, or a little more. Its velocity in the frog is 28m. per second, and the wave length is about 18mm. Ranke* has shown that the lactic acid generated in nerve and muscle consequent upon the active discharge of function, suffices to abolish and even reverse the ordinary nerve current, which is again restored when the acid is neutralized by an alkali. In the nerves the axis-cylinder, and in muscle the intermediate substance, is the seat of the most active chemical changes, and becomes acid; the doubly refracting muscle substance, and the doubly refracting substance of Schwann remain alkaline. Ranke holds that at the point where a stimulus is applied to a nerve, an increased metamorphosis takes place, accompanied by the formation of lactic acid, which causes regular variation of the muscle current, and a state of increased irritability in the nerves.

431. *Electrotonus of Du Bois-Reymond.*—Electrotonus is the alteration produced in the electromotor condition of the whole of a nerve by the passage of a constant current from a battery through part of it. If a portion of nerve-trunk be so placed (Fig. 198), that it touches one of the electrodes by its transverse section (which may be designated T), and the other by its surface or longitudinal section (L), and a portion of its continuation be included in a galvanic circuit, so that a current shall pass in the direction Z—P, which is *the same* in its direction as that between T—L, then the intensity of the "nervous current" T—L, as indicated by the deflection of the needle of the galvanometer,

FIG. 198.

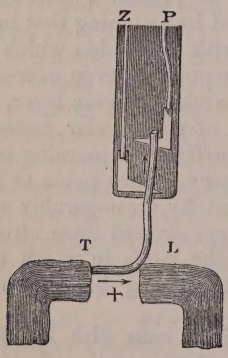
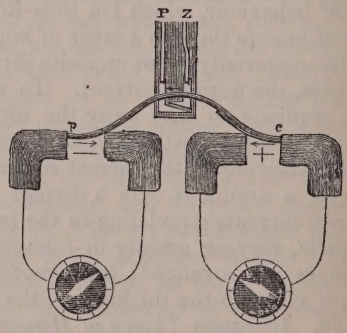


FIG. 199.



will be found to undergo an increase—"positive phase of electrotonus"—the deflection being greater the longer the portion of nerve through which the constant current passes and the stronger that current is; whilst, on the other hand, if the electric current be passed in a contrary direction P—Z, the intensity of the 'nervous current' T—L will decrease — the "negative phase of electrotonus."—The portion Z—P of the nerve, which is included in the electric circuit, is termed the *excited* portion, and the current passed through it is the *exciting current;* on the other hand, the portion T—L included between the electrodes of the galvanometer is the *derived* portion; and the altered condition of this part, which is produced by the extraneous current (this current having been experimentally proved by M. du Bois-Reymond to exert no influence of its own on the galvanometer), is termed the *electrotonic state* of the nerve. By a proper arrangement, the same exciting current may be made to

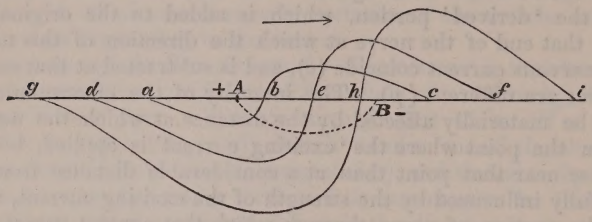
* "Physiologie," 1872, p. 667.

produce the positive phase in one part of a nerve-trunk, and the negative phase in another. Thus if the two extremities of a nerve (Fig. 199, *p* and *c*) be so connected with two galvanometers that both shall develop the 'nervous current,' and an intermediate portion be excited by the transmission of an electric current in the direction Z—P, the nervous current in the 'derived' portion *c* will be increased in intensity, whilst that in the portion *p* will be diminished. Hence it may be inferred, that when any portion of the length of a nerve is traversed by an electric current, besides the usual electro-motive action of the nerve, a new electro-motive action takes place in every point of the nerve by a polarization of its electro-motive elements, which action has the same direction as the exciting current itself; and a current is thus produced in the 'derived' portion, which is added to the original 'nervous current' at that end of the nerve at which the direction of this new current and of the nervous current coincide (*c*), and is subtracted at that end at which the directions are different (*p*). The intensity of the electrotonic condition is found to be materially affected by the distance at which the nerve is examined from the point where the 'exciting current' is applied, being always much greater near that point than at a considerable distance from it. It is also powerfully influenced by the strength of the exciting current, and by the length of the portion of nerve through which that current passes, increasing in intensity with stronger currents, and in proportion to the length of nerve the current has to traverse. These variations in the intensity of the 'nervous current' continue as long as the 'exciting current' lasts, and soon cease when the circuit of that current is broken; a slight enfeeblement of the normal nerve current being apparent for some time after both phases of electrotonus. It is to the induction of the electrotonic state in the nerve supplying it, that the contraction of a muscle is due, which ensues on the completion of the circuit; and to the cessation of this state, that the muscular contraction is due which is consequent upon the interruption of the circuit. Hence the electrotonic changes in the condition of nerves may be observed without previously dividing them.—When, on the other hand, a nerve is 'tetanized' by passing an interrupted and alternating current through a portion of it, the effect is, as in the case of muscle, to produce a *diminution* in its own proper current; the needles of *both* galvanometers, in the arrangement last described, being deflected to the negative side, instead of one going back to zero and the other having its positive deflection increased, as happens when the 'excited portion' is subjected to a continuous and uniform current. The same negative variation of the nervous current has been demonstrated by M. du Bois-Reymond in nerves tetanized by other means, as by the use of strychnia. And the phenomena both of the 'electrotonic state' and of the 'negative variation' are precisely the same, whether motor or sensory nerves be subjected to the experiment; thus making it appear that nerve-force may be transmitted in either direction along each of these orders of nerves. The presence of electrotonus in a nerve may be demonstrated by means of the "physiological rheoscope." For if a portion of nerve, freed from the surrounding tissues, be applied to the sciatic nerve still connected with the muscles of a frog, it will be found that, if the former nerve be excited or stimulated, the muscles in connection with the latter, which is thrown into a state of secondary electrotonus, will contract.

432. *Electrotonus of Pflüger.*—Pflüger has investigated with much care the changes that occur in the excitability of a nerve in a state of electrotonus, or, in other words, through a portion of which an electrical current is passing. Under such circumstances the nerve may be considered to be divided into two

parts, an intra-polar and an extra-polar portion, the latter being again subdivided into that portion situated nearer the nervous centres than the current, or central, and that situated between the current and the muscle, or distal, of the current, the latter being sometimes also called the myopolar portion. As the positive pole of an electrical current is termed the anode, and the negative the kathode, Pflüger has applied the terms anelectrotonus and katelectrotonus to distinguish those conditions established in the portions of nerve in the immediate vicinity of the poles of a constant battery. He has shown that the intra-polar portion of nerve is divided into two zones (Fig. 200); in one of

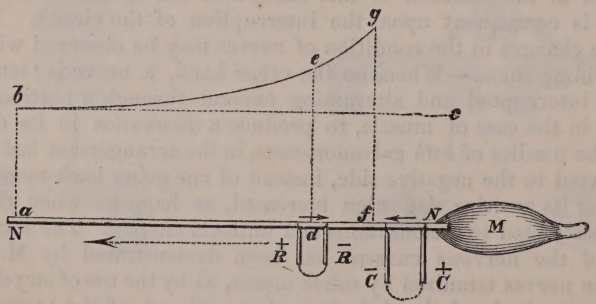
FIG. 200.



A, the Positive, B, the Negative Pole of a constant current applied to a nerve. *a*, *b*, *c*, a curve, showing the effects of a weak current; *d*, *e*, *f*, of a stronger current; *g*, *h*, *i*, of a very strong current. The portion of the curve below the line shows the degree and extent of the depression, the part above of the exaltation of the excitability of the nerve.

these, situated at and near the Positive pole, the excitability of the nerve is diminished, whilst in the other, situated at and near the Negative pole, the excitability is increased. The extent of the portion of nerve in which the

FIG. 201.

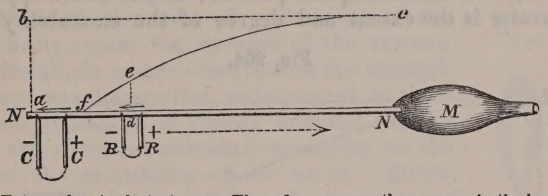


N N, represents a nerve; M, a muscle; C C, the positive and negative poles of a constant current. *a f*, Extra-polar portion of nerve. *d*, Point to which a stimulus, here represented by R R, the positive and negative poles of an interrupted current, but which may be replaced by a mechanical or chemical excitant, is applied. *b*, *c*, indicates the line of normal excitability, supposed for the sake of simplicity to be equal throughout the whole length of the nerve, though in reality it is greater, and should therefore ascend towards *b*. *b*, *e*, *g*, indicates the curve of augmented excitability in the extra-polar portion of nerve, the amount of increase being greatest at the kathode—as at *g*, less marked at *e*, and falling to its ordinary amount at *b*.

excitability is lowered, the positive or anelectrotonic zone, is small in proportion to the weakness of the current; whilst the negative or katelectronic zone, in which the excitability is exalted, is correspondingly large; so that, with very weak currents, nearly the whole of the intra-polar portion of the nerve is in a state of exalted excitability, whilst with strong currents the intra-polar portion of the nerve is almost wholly in a state of depressed excitability. The same conditions of exalted or depressed excitability also extends for a considerable distance beyond the poles—*i.e.*, in the extra-polar portions of the nerves in

both directions. The mode of determining the variations in the excitability of the nerve at the two poles may be understood with the aid of the diagram (Fig. 200). In Fig. 201, c c represents the poles of the constant or polarizing currents by means of which the state of electrotonus is established, and R R those of the exciting current, or that by means of which the excitability of the nerve is tested; the latter may be replaced by a mechanical stimulus. Eckhard employed a solution of common salt. Before throwing the nerve into an electrotonic state by the application of the poles of the constant current, a few trials are made to ascertain what is the weakest stimulus which, when applied at *d*, will produce contraction in the muscle. When this is known,

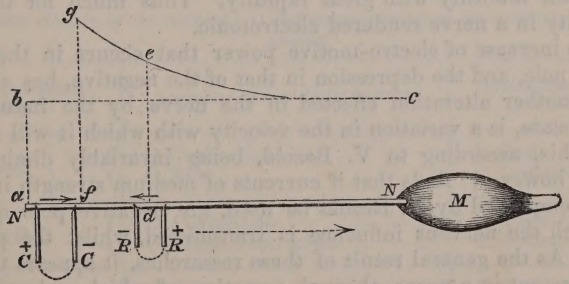
Fig. 202.



Centrifugal Extra-polar Anelectrotonus. The references are the same as in the last Fig., except that *a f* represents the intra-polar portion of the nerve, and that the curve of diminished excitability is represented by *f*, *e*, *c*; the lowest degree being at the anode, *f*, and the nerve gradually recovering its normal excitability towards *c*.

the constant current is applied, and it will then be found that if the direction of this be as in Fig. 201, either a much weaker stimulus applied at *d* will produce contraction in the muscle, or the same stimulus will produce a much

Fig. 203.

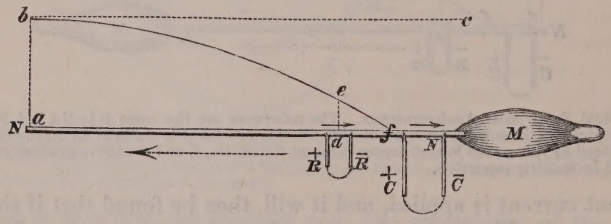


Extra-polar Centrifugal Katelectrotonus. The increase in the excitability of the nerve is shown by the curve, *g*, *e*, *c*, to be greatest in the vicinity of the kathode of the polarizing current, c, c.

more vigorous contraction, in either case showing that the excitability of the nerve has been increased. This is expressed by the curve *b*, *e*, *g*. If an electrical stimulus is employed, the current should be passed in the direction indicated, as in that case it would tend to reduce the influence of the kathode of c c, and by so much render the results obtained more striking. This constitutes Pflüger's extra-polar centripetal katelectrotonus. By a similar mode of proceeding, the excitability of the nerve behind the ascending current, or in the myopolar portion, which is under the influence of the positive pole of the constant current, c c, can, as by the curve *f*, *e*, *c* in Fig. 202, be shown to be remarkably diminished. This constitutes Pflüger's extra-polar centrifugal anelectrotonus. The curve *g*, *e*, *c*, in Fig. 203 shows the variation in the excitability in the myopolar portion of the nerve, when the Negative pole is next the muscle. Lastly, Fig. 204 shows the condition of excitability in the nerve

in centripetal extra-polar anelectrotonus. Pflüger found that in all these cases the strength of the polarizing current was of great importance, and that within certain limits the increase of excitability near the kathode, and the decrease near the anode, augmented; but that, if these limits be passed, and currents of much greater strength than usual were employed, the phenomena were less marked, and at length failed altogether to occur. From an examination of the curved lines in the preceding figures, it will also be seen that the excitability of the nerve varies with the distance of the part examined from the electrode, the increase or diminution being always greatest at the kathode and anode respectively, whilst the effect diminishes as these are receded from. There is one other circumstance that affects the excitability of the nerve—namely, the length of the intra-polar portion; and it would appear the longer this is, the greater is the extent and degree of the excitability of the nerve

FIG. 204.



Centripetal Extra-polar Anelectrotonus. Here, as indicated by the curve, *b*, *e*, *f*, the excitability of the nerve falls as the positive pole or anode of the polarizing current is approximated.

around the kathode. As regards time, the state of increased excitability always attains its full intensity with great rapidity. Thus much for the variations of excitability in a nerve rendered electrotonic.

433. The increase of electro-motive power that occurs in the vicinity of the positive pole, and the depression in that of the negative, has already been noticed. Another alteration effected in the nerve by the induction of the electrotonic state, is a variation in the velocity with which it will conduct impressions; this, according to V. Bezold, being invariably diminished. Dr. Rutherford, however,* finds that if currents of medium strength instead of the strong ones employed by V. Bezold be used, the negative pole quickens the rate at which the nervous influence is transmitted, whilst the positive pole retards it. As the general result of these researches, it appears then that the conditions present in a nerve, through a portion of which a closed continuous current is passing, and which is, therefore, in a state of electrotonus, are such that at the anode or positive pole of the current there is an exaltation of the intensity of the ordinary nerve-current (positive phase), and depression of the excitability (anelectrotonus), and of the conductivity or velocity of transmission of impressions. On the contrary, at the kathode there is constantly a depression of the intensity of the ordinary nerve-current (negative phase), and coincident exaltation of the excitability (katelectrotonus) and of the conductivity.†

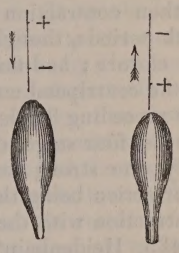
434. From the foregoing observations it will be intelligible that the action of electrical currents applied to nerves in producing muscular contraction is

* Humphry and Turner's "Journal of Anat. and Phys.," vol. ii. 1868, p. 95.

† A very different explanation of the phenomena of electrotonus, founded on chemical considerations, has been suggested by Hermann (see his "Untersuchungen," published at Berlin in 1867); but his views have been vigorously assailed in an able paper by Du Bois-Reymond, in the "Berichte der Berlin. Akadem.," 1867, p. 597.

liable to many variations, and that numerous circumstances must be taken into consideration before an explanation can be given of any particular phenomenon. Thus it has long been well known that though contraction of a muscle usually occurs at the moment of opening and closing a current of electricity transmitted through its motor nerve, yet that this is not constant, the contraction failing sometimes at the moment of closing and sometimes at the moment of opening the current. The singularity of this phenomenon has attracted the attention of many observers;* and it is now ascertained that the effects produced upon the muscle are dependent—1st, upon the direction of the electrical current passed through the nerve, whether centrifugal—*i.e.*, from the origin to the periphery of the nerve (Fig. 205), or centripetal—*i.e.*, from the periphery towards the origin (Fig. 206); 2ndly, upon the state of excitability of the nerve; and 3rdly, upon the strength of the current. Ritter and Nobili, in whose observations the strength of the current was disregarded, endeavoured to show that a definite succession of results followed the application of the electrical stimulus, according to the direction and the excitability of the nerve. Ritter, operating on Frogs, the excitability of whose nerves departed slowly after death or excision, was able to distinguish six stages; whilst Nobili, operating in the warmer climate of Italy, could distinguish only four. The following tabular arrangement taken from Funke will show the relations of the contraction of the muscle to the degree of excitability remaining in the nerve, and to the direction of the current:—

Fig. 205. Fig. 206.



Ritter and Nobili's Law of Contraction.

C *indicates closure of the current;* O *indicates opening of the current, or breaking contact.*

Grade of Excitability of the Nerve.	Ascending or Centripetal Current.	Descending or Centrifugal Current.
I. (Ritter)	C, Contraction O, Rest	C, Rest. O, Contraction.
II. (Ritter)	C, Contraction O, Slight Contraction	C, Slight Contraction. O, Contraction.
III. (Ritter) I. (Nobili)	C, Contraction O, Contraction	C, Contraction. O, Contraction.
IV. (Ritter) II. (Nobili)	C, Weak Contraction (Ritter) / Rest (Nobili) O, Contraction	C, Contraction. O, Slight Contraction.
V. (Ritter) III. (Nobili)	C, Rest O, Contraction	C, Contraction. O, Rest.
VI. (Ritter) IV. (Nobili)	C, Rest O, Rest	C, Slight Contraction. O, Rest.

From this Table it is apparent that in the highest grade of excitability of the nerve, the centripetal current induces contraction only on closure of the current,

* As of Ritter and Nobili, Matteucci, Du Bois-Reymond, Eckhard, and Pflüger.

none occurring on opening it. Contraction on opening the current first happens in the second stage—*i.e.*, when the excitability of the nerve is somewhat diminished, and is then only feeble. In the 3rd stage of excitability of Ritter, the 1st of Nobili, the vigour of the opening and closing contraction is about equal. In the 4th grade, the closing contraction is weak, the opening strong. In the 5th stage, there is no contraction on closure, but it occurs on opening the current; whilst in the 6th and last stage no contraction follows either the closure or the opening of the current. For the descending or centrifugal current, the phenomena present themselves in an inverse order,—in the first or highest stage of excitability, there is contraction only on opening the current—then weak contraction on closure, as well as contraction on opening—then contraction of equal strength at both periods—then contraction at both periods, though weaker on opening the current—then contraction only on closure; and finally, in which respect it differs slightly from the effects of the centripetal current, weak contraction on closure of the current. From the preceding Table, the statement of Nobili, who only experimented during the last four stages of irritability, becomes intelligible, that there is essentially only one strong contraction for each direction of the current; an opening contraction being the most marked with the centripetal current, and a closing contraction with the centrifugal current.

435. Heidenhain* and Pflüger,† following up this train of research, showed that in freshly-prepared nerves, whose *excitability was therefore of the highest grade*, the law of contraction was dependent upon the strength of the current; and the phenomena have been thus formularized by Pflüger:—

Strength of Current.	Direction of Current.	
	Centripetal.	Centrifugal.
Weak . . . {	C, Contraction . . O, Rest	C, Contraction. O, Rest.
Moderate . . {	C, Contraction . . O, Contraction . .	C, Contraction. O, Contraction.
Strong . . . {	C, Rest . . . . . . O, Contraction . .	C, Contraction. O, Weak Contraction.

Thus beginning with currents so feeble that no contraction is induced either on making or on breaking contact in very excitable nerves, Pflüger found that on passing a slightly stronger, but still weak current, in a centripetal direction, contraction first occurs on closure, but none on opening. With currents of moderate strength, contraction occurs both on closing and opening the current; and lastly, if the current exceeds a certain strength, no contraction occurs on closing, though it is well marked on opening the current. If the same experiments are repeated with the centrifugal current, we obtain with the weakest current contraction on closure alone (exceptionally also on opening); with moderately strong currents, contraction both on opening and closure; and with strong currents, the closing contraction preponderates with centrifugal currents, and the opening contraction with centripetal. As regards the reactions of sensory nerves, it is maintained by Pflüger that the effects

* Heidenhain in "Archiv f. Phys. Heilk," 1857, p. 442.

† Pflüger, "Archiv f. Path. Anat.," Band xiii.; and "Untersuchungen über d. Physiologie des Electrotonus," Berlin, 1859.

produced by electrical stimulation are dependent upon the force of the current, except that, as might be expected from the direction in which they ordinarily conduct their impressions a kind of inverse relation exists.

436. Those who hold with Hermann and Onimus, with whom Ranke is to some extent in accord, that many of the electric phenomena presented by nerve and muscle are dependent upon chemical action, extend this view to the explanation of the different conditions of electrotonus. Onimus,* for example, refers to an experiment made by Matteucci, which consists in covering a platinum wire a yard in length with tow. The wire is dipped in salt, and arranged as in the experiment for showing electrotonus. On passing a current of electricity through a given portion of it, a strong electrotonic condition is established, even at a distance of eighteen inches or more. It would hence appear that the electrotonic state is not one that is peculiar to the nerves, and this part of the subject has been carefully worked over by Hermann.† They further offer a very simple explanation of the anelectrotonic and katelectrotonic zones of Pflüger. They contend that the passage of an electric current through a nerve is attended by an electrolytic action resulting in the formation of acids around the positive pole and of alkali around the negative, which is sufficient to explain all the phenomena, since acids lower whilst alkalies exalt the excitability of the nerve. Pflüger, from the results of his experiments, laid down the following law :—A certain length of nerve being given, this is excited by the supervention of katelectrotonus and by the disappearance of anelectrotonus; but it is not excited by the disappearance of katelectrotonus nor by the supervention of anelectrotonus. This law has been slightly modified by Cyon, who formulates it as follows :—A nerve is excited when its molecules pass from their ordinary state to one of greater mobility (katelectrotonus), or when they pass from a state of less mobility (anelectrotonus) to the ordinary state. The nerves do not, on the contrary, experience any excitation, either when they pass from their ordinary to a state of less mobility (anelectrotonus) or on their passage from a state of greater mobility (katelectrotonus) to their ordinary state.‡ Onimus maintains that the practical value of these facts rests in remembering two well-established points—First, that the descending or direct current is that which acts most energetically on motor nerves, or, in other words, the descending current is that which most strongly calls forth muscular contraction; and secondly, that every current when applied to a nerve determines a current in the opposite direction at the moment of its cessation. Thus each time that a nerve is electrified with an ascending current a descending current is developed at the moment of breaking in the interior of the nerves, and contrariwise at the moment when a descending current is broken an ascending current is formed. In accordance with this, Onimus gives the subjoined table, obtained by electrifying nerves without the direct application of the poles to the nerve, which he contends interferes with the results, since it causes local electrolytic action. It will be seen to resemble the scheme given by Nobili.

* Robin's "Journal de l'Anatomie," 1874.
† "Handbuch.," 1879, p. 175.
‡ Cyon, "Principes d'Electrothérapie," 1873, p. 103.

		Descending Current.	Ascending Current.
1. Period	Closure	Contraction	Contraction.
	Opening	Contraction	Contraction.
2. Period	Closure	Contraction	Feeble Contraction.
	Opening	Feeble Contraction	Contraction.
3. Period	Closure	Contraction	O
	Opening	O	Contraction.
4. Period	Closure	Contraction	O
	Opening	O	Feeble Contraction.
5. Period	Closure	O	O
	Opening	O	Feeble Contraction.

Thus, in the first period, the excitability of the nerve being undiminished, contraction of the muscle takes place as soon as the molecular state of the nerve undergoes alteration, which occurs both at the moment of closure and of breaking of the current; but by degrees, as the excitability of the nerve diminishes, contraction takes place only on the closure of the descending current, and on the opening of the ascending current. But the breaking of the ascending current is equivalent to the formation of a descending current, so that as the third period is reached the muscle only contracts with a descending current. In the same way, at the moment of breaking a descending current an ascending current is formed which remains without action on the muscles like the ascending current of the battery. At the fourth period the ascending current only gives the contraction of opening when the current has been applied for some time, for then the (descending) polar current becomes more energetic. At the fifth period, when the current of the battery no longer gives any contraction, this may still be sometimes obtained by the polar current. Thus Onimus maintains that by taking into consideration the formation of a polarizing current, and the greater action of the descending current, all the phenomena of Pflüger's alternations admit of ready explanation.* Grützner's† observations and experiments have led him to the conclusion that centripetal nerve fibres are stimulated by heat and by the constant current, apart from the opening and closing of the current, but of the centrifugal fibres only those are stimulated by the constant current which dilate the cutaneous vessels. The secretory and motor nerves are not persistently affected by the constant current.‡

2. *Of the Spinal Cord and Medulla Oblongata;—their Structure and Actions.*

437. In our more detailed consideration of the functions of the several divisions of the Nervous System, it is desirable, for several reasons, to com-

* Dr. Radcliffe, who has paid much attention to the subject of electrotonus, notes various facts which make it difficult to believe that the electrotonic movements of the needle have to do, as Du Bois-Reymond supposes, with changes in the nerve-current, produced by the action of the electrotonizing current upon the nerve. His conclusions are contained in his work entitled "Dynamics of Nerve and Muscle," post 8vo, Macmillan and Co., 1871; and "Vital Motion a mode of Physical Motion."

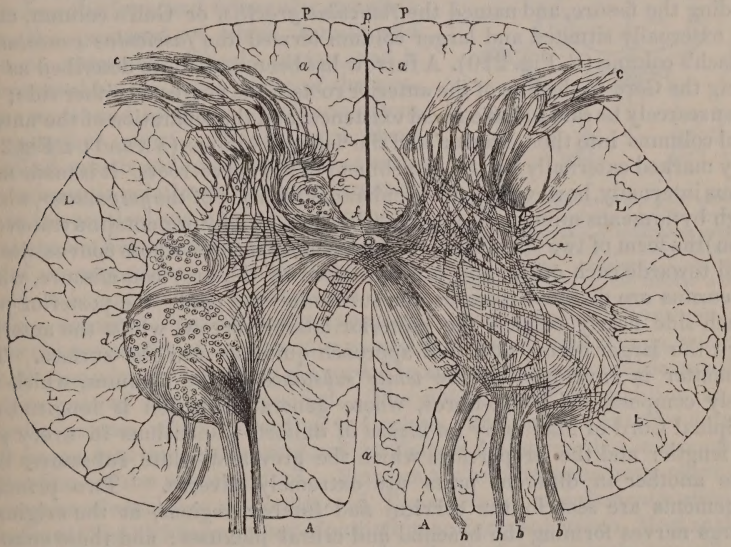
† Pflüger's "Archiv," 1878, p. 249.

‡ See for an account of Hermann's present views on Electrotonus, a translation of his paper entitled 'Die Ergebnisse neuerer Untersuchung,' &c., in Foster's "Journal of Physiology," vol. i. 1878, p. 196.

mence with the *Cranio-Spinal Axis;* which, as already pointed out, may be considered as constituting the fundamental portion of this apparatus. The entire Axis is divided into its Cranial and its Spinal portions, the passage of the Cord through the 'foramen magnum' of the occipital bone being considered to mark the boundary between them; and although the separation of the Medulla Spinalis from the Medulla Oblongata, which is thus established, is in itself purely artificial, yet it will be found to correspond completely with the natural division founded on their respective physiological attributes.

438. The *Spinal Cord*,* which extends from the margin of the foramen magnum to the first or second lumbar vertebra, and which is prolonged as the *filum terminale*† to the extremity of the sacral canal, is almost completely

FIG. 207.



Transverse section of *Spinal Cord*, through the middle of the lumbar enlargement, showing on the right side the course of the nerve-roots, and on the left the position of the principal tracts of vesicular matter:—A, A, anterior columns; P, P, posterior columns; L, L, lateral columns; *a*, anterior median fissure; *p*, posterior median fissure; *b*, *b*, *b*, *b*, anterior roots of spinal nerves; *c*, *c*, posterior roots; *d*, *d*, tracts of vesicular matter in anterior column; *e*, tracts of vesicular matter in posterior column, termed by Jacubowitsch the "sympathetic" column or tract; *f*, central canal, surrounded by the grey commissure; *g*, substantia gelatinosa of Rolando.

divided by the *anterior* and *posterior median fissures* (Fig. 207, *a*,*p*), into two lateral and symmetrical halves. The 'anterior median fissure' (*a*) is more distinct than the posterior, being wider at the surface; but it only penetrates to about one-third of the thickness of the Cord, its depth increasing, however, towards its lower part. The sides of the 'posterior median fissure' (*p*), on the other hand, are in closer approximation; but the division commonly

* The sketch given in the text of the Anatomy of the Spinal Cord, is chiefly derived from the statements of Prof. Kölliker, in his "Mikroskopische Anatomie" (Band ii. §§ 115, 116), and of Mr. J. L. Clarke in the "Philosophical Transactions," 1851, 1853, and 1859; but Gerlach gives an excellent account of it in Stricker's "Hum. and Comp. Histology," Syd. Soc. Transl., vol. ii. p. 327.

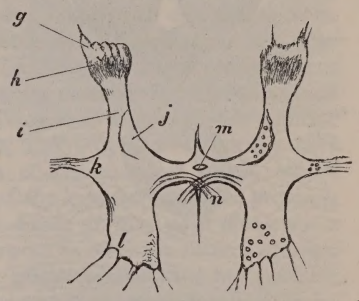
† The structure of the 'filum terminale' is in every respect essentially the same as that of the proper Spinal Cord, save that no nerve-roots are connected with it.

extends to about half the thickness of the cord, being deeper towards its upper than towards its lower end. The two halves, therefore, are only united by a commissural band, which occupies the central part of the cord; and this is traversed by the 'Spinal canal' (*f*), which is continued downwards from the fourth ventricle, is about 1-100th of an inch in diameter, and, according to Lockhart Clarke, is lined with a layer of columnar ciliated cells, whose attached extremities taper into delicate fibres, and become continuous with the fibres of the connective tissue of the white columns.—At a little distance from either side of the posterior median fissure, and corresponding with the line of attachment of the posterior roots of the nerves, is the *posterior lateral furrow;* a shallow, longitudinal depression, which marks out the 'posterior columns' of the Cord (P, P) as distinct from the 'antero-lateral columns.' In the cervical and dorsal regions the posterior column is itself divided into a fasciculus (*c*, Fig. 210) bounding the fissure, and named the *funiculus gracilis*, or Goll's column, and a more externally situated and larger column termed the *fasciculus cuneatus*, or Burdach's column (*d*, Fig. 210). A furrow has been sometimes described as traversing the Cord in the line of the anterior roots of the nerves on either side; but this can scarcely be said to have a real existence; and the separation of the 'antero-lateral columns' into the 'anterior' and the 'lateral' columns (A A and L L Fig. 207) is only marked externally by the attachment of the nerve-roots. It is made more obvious internally, however, by the peculiar distribution of the *grey matter*, which, though by no means uniform throughout the Cord, usually presents (in a transverse section) the form of two somewhat crescent-shaped masses, whose convexities are turned towards each other, and are connected by the grey commissure, whilst their cornua are directed towards the surface of the cord; the posterior peak on each side nearly reaches the posterior lateral furrow, whilst the anterior, though the larger cornu, does not approach quite so near the surface. The grey matter is enveloped by the *white substance* of the columns, which are entirely composed of nerve-fibres, whose general direction is longitudinal. The Spinal Cord of Man is by no means of uniform dimensions in every part of its length: and the proportions which the grey and white substances bear to one another in different parts are extremely diverse. Two principal enlargements are seen in the cervical and lumbar regions, at the origins of the large nerves forming the brachial and crural plexuses; and these enlargements are chiefly due to an increase of the *grey* substance, which is comparatively deficient in the intervals. On the other hand, there is a regularly-progressive increase in the *white* substance, as we proceed from the lower to the higher portion of the cord; and this fact of itself serves to indicate the probability, that the longitudinal columns serve (as formerly supposed) to establish a direct connection between the Encephalic centres and the ganglionic cells from which the roots of the Spinal nerves arise or with these roots themselves.

439. The *grey matter* or *vesicular substance* of the Spinal Cord, which is best seen in transverse section (Figs. 207 and 208), is by no means uniform in its texture throughout. Its *anterior cornua* (*d*, Fig. 207 and *l*, Fig. 208), which are thicker and shorter than the posterior, are of a uniform grey colour; and they consist of large, well-developed nerve-cells, which usually present many radiating processes, one of which generally passes into the anterior root of the nearest spinal nerve; whilst another ascends on its own side, and others form communications either with adjoining cells or with those in the horn, or on the opposite side of the Cord. The cells of the anterior horn connected together in this way form groups which may reasonably be supposed to constitute centres for the numerous fibres distributed to each muscle, so that an impulse of the will or other stimulus acting upon one of the cells may

excite the whole to equal and consentaneous action, and thus abolish the necessity that would otherwise exist for every muscular fibre to possess its own motor nerve direct from the brain. The central portion, which contains the canal, and which also forms the commissure, has a similar composition; but the cells are smaller, though still having long branching radiations; and the fibres are extremely fine, their tubularity being often indistinguishable. The *posterior cornua* (Fig. 208 *g*, *h*, *i*, *j*) are longer and narrower than the anterior, and each is divided into a caput and a cervix cornu.* The caput or bulbous extremity of the horn consists of an outer and comparatively transparent gelatinous portion, named the *substantia gelatinosa* of Rolando, similar in structure to the grey substance surrounding the central canal. It contains numerous fusiform and triangular ganglion cells, the processes of which ramify and form an extremely delicate plexus, and it is traversed by the nerve fibres of the posterior roots, and by fibres which arise from the ganglion cells. Mingled with these are blood-vessels and some connective tissue. The substantia gelatinosa attains its greatest size in the cervical and lumbar enlargement, that is, at the points, where the largest number of sensory nerves enter the cord. By some† it is regarded as a tissue of a supporting nature. The *substantia spongiosa* forms the remainder of the posterior as well as of the anterior cornua, and constitutes the most important part of the cord. It contains numerous multicaudate cells, the processes of which are ramified. The cells give off in addition an axis-cylinder process, which, according to Gerlach, runs into the anterior cornu and then passes into the *anterior* root, whilst Deiters maintains that it is continuous with a fibre of the *posterior* root. Between the cells are numerous nerve fibres, the course of which has not been traced. The *median or commissural portion* of the spinal cord (Fig. 205) is composed of both white and grey substance. Most anteriorly and forming the bottom of the anterior longitudinal fissure is the anterior white commissure, which is chiefly composed of decussating fibres. Some of these are derived from the anterior columns, and from the anterior roots of the spinal nerves of the opposite half of the cord, which probably ascend in the antero-lateral columns, or join the median motor ganglion cells of the opposite side, others are commissural between the anterior cornua, and others again appear to come from the posterior roots. Besides these the anterior white commissure contains some longitudinal fibres. Behind the anterior white commissure is the anterior grey commissure (*h*), and the broader posterior grey commissure (*g*), which forms the bottom of the posterior longitudinal sulcus, with the central canal and surrounding gelatinous substance between them. The fibres forming the posterior grey commissure pursue a course that seems to show they are connected with the posterior roots of the spinal nerves, and with the cervix cornu posterioris of the opposite side. There is therefore here also a decussation of fibres. Situated a little in front of the exact centre is the central canal (Figs. 208 *m*, 209 *c*). This is a minute passage, the cavity of which in the adult

Fig. 208.



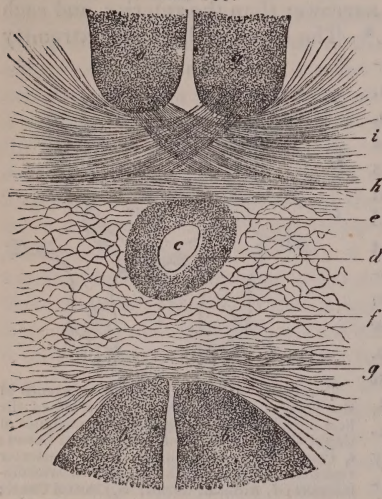
Transverse section of the grey substance of the *Human Spinal Cord* at the level of the first dorsal Nerves:—*g*, gelatinous substance of Caput Cornu; *h*, dark interior of Caput Cornu; *i*, Cervix Cornu, containing, *j*, the posterior vesicular column; *k*, the tractus intermedio-lateralis; *l*, Anterior Cornu; *m*, Central Canal; *n*, Anterior Decussating Commissure.

* See Lockhart Clarke, "Phil. Trans.," 1858, p. 249. Gerlach, Art. 'Spinal Cord,' in Stricker's "Human and Comp. Histology," vol. ii. p. 355, 1872.

† Schwalbe, "Lehrbuch der Neurologie," 1880, p. 347.

is usually obliterated with cells, but which in childhood is lined by a layer of ciliated columnar cells, the attached extremities of which, named the ependyma fibres, dip into a layer of gelatinous tissue resembling the substantia gelatinosa of Rolando. The major part of this substance is finely granular, the dots being probably the cut ends of fibrils, and besides the radiating fibres of the columnar central cells, some concentric fibres may be seen, with a few scattered nerve fibres and stellate cells. A remarkable column of ganglionic cells, constituting the inner and anterior part of the Cervix cornu (*j*, Fig. 208), and extending from the lower part of the cord to the middle of the cervical enlargement where it terminates, has been described by Clarke under the term of the *posterior vesicular column.** The point of junction of the anterior and posterior cornua (*k*) is termed by the same observer the *tractus intermedio-lateralis*. It extends from the upper roots of the eighth cervical nerves to the lowest part of the dorsal region, but is most prominent about the first and second dorsal nerves. The posterior vesicular columns, on the other hand, are largest at the lowest part of the dorsal region. The delicately fibrillated and granular nucleated substance which intervenes between the axis-cylinders of the grey substance of the spinal cord and forms the greater part of it, termed 'neuroglia' by Virchow, 'reticulum' by Kölliker, 'granular basement substance' by Henle, and 'spongy substance' by Schultze, is believed by Henle,† Robin,‡ and others to be quite distinct from connective tissue, not only in function, but in miscroscopical characters and in chemical reactions.§ It is chiefly found in the grey substance of the nervous centres, and it immediately surrounds the central canal of the cord.‖ It is an almost transparent material of grey colour, and of finely granular aspect¶ like the matrix of hyaline cartilage, with little clumps of cytoid bodies (myelocytes) scattered through it, which seem to be in connection with the cells lining the central canal and with the pia mater. Pervading every part of the neuroglia of the grey substance of the cord, except that lying in immediate proximity to the central canal, is a close plexus of extremely-fine fibres, chiefly derived from the processes of the nerve cells just described. The blood-vessels of the central parts of the nervous system are surrounded by a loose sheath, between which and the proper external coat

Fig. 209.



Median portion of a transverse section of the spinal cord of a child six months old, from the lower part of the cervical region, treated with the double chloride of potassium and gold. Magnified 500 diameters. *a, a*, anterior columns. *b, b*, posterior columns. *c*, central canal. *d*, line indicating the epithelium of the central canal. *e*, connective tissue, sometimes called the jelly or grey substance of Stilling, or *substantia gelatinosa centralis*, surrounding the central canal. *f*, nerve fibre plexus around the central canal. *g*, transverse fibres of the posterior grey commissure, most numerous in the sacral and cervical regions. *h*, transverse fibres of the anterior grey commissure. *i*, decussation of fibres in the anterior white commissure.

* These constitute the dorsal nuclei of Stilling and the respiratory centres of W. Krause.

† "Centralblatt," 1869, p. 117. ‡ "Anatomie et Physiologie Cellulaire," 1873, p. 117.

§ Gerlach, Stricker's "Hum. and Comp. Histol.," Syd. Soc. Trans., vol. ii. p. 335. Frey ("Histology." Barker's Transl., p. 575) and Toldt ("Lehrbuch der Gewebelehre," 1877, p. 197), however, still regard it as a special form of connective tissue.

‖ The "noyau periépendymaire" of the French writers.

¶ Gerlach, "Centralblatt," 1867, Nos. 24 and 35.

lymph corpuscles are perceptible.* These spaces His considers to represent the lymphatic system of these parts, which are otherwise destitute of this system of vessels.

440. The connection of the Nerve-roots of the Spinal Nerves with the several components of the Cord, and the course of the fibres after entering it, may be made out partly by means of *sections*, and partly by following the course of individual fibres by ordinary microscopical dissection.† The following is an outline of the information which may thus be gained from a comparison of transverse and longitudinal sections (Fig. 207 *et seq.*).—The bundles that form the Posterior roots (Fig. 205, *c*, *c*) consist of three sets, which differ from each other partly in direction, and partly in the size of their component filaments. The *first* set (which are more numerous in the upper part of the Cord), enter the posterior columns horizontally; and then, taking a longitudinal direction *down* the Cord, send fibres into the anterior grey substance, of which some bend upwards, and others downwards; part apparently becoming continuous with fibres of the anterior roots; whilst another part lose themselves among the fibres of the anterior columns, in which they may either proceed continuously to the head, or may pass along for a limited distance only, to emerge in the nerve-roots of some other segment. The *second* set of bundles also traverse the posterior columns horizontally and obliquely inwards; their further course may be best traced in a transverse section (Fig. 207). These fasciculi, which are composed of remarkably fine and delicate fibres, interlace so as to form with each other an intricate plexus; and from this, straight and distinct bundles enter the posterior cornua along their whole breadth, crossing the 'substantia gelatinosa' both obliquely and at right angles. Having thus entered the vesicular substance of the Cord, some of the fibres become connected with multipolar ganglionic cells; others, after traversing it, emerge from it again, into either the posterior columns, or the posterior portion of the lateral columns; others pass towards the transverse commissure, through which they seem to make their way to the posterior lateral columns of the opposite side; and others, again, form a fine network, which extends towards the anterior cornua. Of the fibres of a *third* set, a part seem to become directly continuous with the fibres of the posterior columns; the larger proportion of them, however, cross these columns obliquely upwards, and enter the grey substance at different points; after passing into which, they can no longer be clearly followed, although some of them appear to form loops and then return to the white columns.—The fasciculi of fibres which constitute the Anterior roots (Fig. 207), on the other hand, traverse the anterior columns of the Cord nearly horizontally, and in straight and distinct bundles, which do not interlace with each other until they reach the anterior cornua of the grey substance; on entering this, they break up into smaller bundles and separate fibres, which diverge in various directions, but, in the lumbar and cervical enlargements, where their course can be most distinctly followed, run in three main directions, laterally, directly backward, and towards the middle line; in each of these groups many fibres may be found which unite with the large multipolar ganglionic cells of the anterior horns of the grey substance; whilst some are believed to pass out again into the anterior, and others into the lateral columns of the same side, without entering any ganglion cell, but ultimately crossing to the opposite side at the decussation of

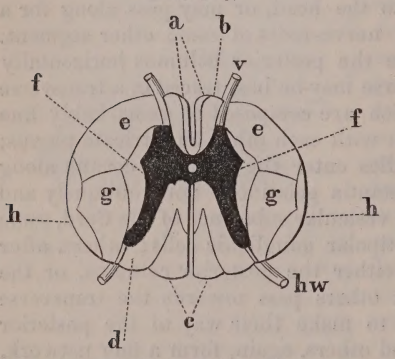
* His in Siebold and Kölliker's, "Zeitschrift," Band xv. 1865, p. 127.

† J. L. Clarke succeeded, by the adoption of a peculiar method of preparation (for which see "Phil. Trans.," 1868, p. 321), in making sections of considerable thickness sufficiently transparent to allow the course of the fibres and the contour of the nerve-cells and their prolongations, to be distinctly made out.

the pyramids. The statement that the fibres are not connected with any cell requires, however, confirmation. Other fibres, again, pass towards the anterior part of the commissure, in which they cross over to the opposite side, entering into connection with the cells of the anterior cornu, or ascending in its anterior and lateral columns; a considerable number plunge into the central substance of the grey cornu, and of these some become longitudinal, passing equally upwards and downwards, whilst others seem to traverse it horizontally, so as to come into relation (not improbably, through the intermediation of ganglion cells, into actual continuity) with the posterior roots.*

441. Thus we see that there are two very distinct courses pursued by the root-fibres of the Spinal Nerves, in the substance of the Cord; the first *transverse*, the second *longitudinal*. The fibres belonging to the former category traverse the Cord horizontally or obliquely, and appear to be connected with the other set of roots connected with the same segment, either on its own or on the opposite side of the median fissure. Of those belonging to the latter, a small part appears to connect the posterior roots directly with the posterior columns, without passing into the vesicular substance; but the remainder of those belonging to the posterior roots first enter the grey matter of the Cord, and then emerge from it either into the posterior column, or into the posterior part of the lateral column of their own or of the opposite half of the Cord; and, in like manner, all the longitudinal fibres belonging to the anterior roots first enter the vesicular substance, and either terminate in the ganglionic cells in the anterior horn or re-enter the anterior column, or the anterior part of the lateral column, of the same or of the opposite side. The longitudinal fibres of the Cord taken collectively form a series of fasciculi or columns which probably possess definite functions, since, in the process of development, certain fasciculi obtain their myelin investment at different periods, whilst, on section of the whole Cord, certain fasciculi alone degenerate above and below the section, and, in cases of disease of certain parts of the brain, particular fasciculi alone atrophy. An attempt to represent the position of these fasciculi has been made by Flechsig (see the accompanying wood-cut Fig. 210). The anterior column is divided into the *pyramidal* fasciculus (*a*), which immediately

Fig. 210.



A section of the Cord at the seat of the 3rd dorsal vertebra. The black central portion represents the grey matter of the cord; *v*, anterior root; *h*, *w*, posterior root; *a*, *g*, pyramidal columns; *b*, basal fasciculus of anterior pyramid; *c*, Goll's fasciculus; *d*, Burdach's fasciculus, or fasciculus cuneatus; *e* and *f*, mixed fasciculi of lateral columns; *h*, lateral cerebellar columns.

* Those who are desirous of pursuing the structure of the Spinal Cord in more detail than can possibly be given in a general survey like the present, are referred to the important work published by Stilling in 1856, entitled "Neue Untersuchungen über den Bau des Rückenmarks," in 3 parts, with an atlas; also to the "Untersuch. über den feineren Bau des Central Nerven-system des Menschen," by J. v. Lenhossek, Wien, 1855; to the researches of Bidder and Kupffer, "Ueber die Textur des Ruckenmarks," Leipzig, 1857; to the valuable papers in the "Philosophical Transactions" for 1851, 1853, 1858, part i. p. 231, 1859, part i. p. 437, by J. Lockhart Clarke; to the Translation by the Sydenham Society of the treatise of Schröder v. d. Kolk, 1859; and to the essays of Dr. C. Frommann, "Untersuch. üb. die Norm. u. Path. Anat. des Ruckenmarks," Jena, 1864, 4 plates; the work of J. Luys, "Recherches sur le Système Nerveux Cérébro-spinal," Paris, 1865; Gerlach, in Stricker's "Human and Comp. Histology," Syd. Soc. Trans., 1872 p. 327; Pick, "Centralblatt," 1878, p. 20.

bound the anterior fissure, and the more externally situated proper or *fundamental* fasciculus. The posterior column contains the *fasciculus gracilis* of Goll (*c*) and the *fasciculus cuneatus* of Burdach (*d*). The lateral columns are composed of the anterior (*e*) and the lateral mixed fasciculi (*f*), the pyramidal fasciculus (*g*), and, lastly, (*h*,) the lateral cerebellar fasciculus. Of these, *a* and *g* are the fasciculi which contain all the connecting fibres between the grey substance of the Cord and the ganglion of the pes cerebri, which pass onwards to the central convolutions of the cortex of the Cerebrum; *h*, composed of coarse fibres, connects Clark's column in the grey substance of the Cord with the Cerebellum; *b*, *e*, and *f* are composed of fibres connecting the reflectorial centres in the grey substance of the Cord and in the medulla oblongata, and also the fibres which constitute the upward prolongations of the anterior roots, and which by degrees enter the grey matter of the Cord; *c* is composed of fibres which connect the posterior roots of the spinal nerves with the grey nuclei of the *funiculi graciles* of the medulla oblongata; *d* is composed of fibres connecting the posterior roots with the grey matter, as well as fibres connecting both these with the retiform nucleus in the medulla oblongata. The fasciculi *a*, *g*, *h*, and perhaps also *c*, present a progressive increase in sectional area in passing from below upwards, which is in accordance with the view that they connect intra-cranial central regions with ganglionic centres distributed in the grey substance of the Cord. The fasciculi *h*, *d*, and *e* vary in size in different parts of the Cord, in correspondence with the number and size of the nerve-roots entering them; hence we may conclude that these fasciculi contain fibres which connect different parts of the Cord with each other and with the medulla oblongata, but do not pass up directly to the higher parts of the cerebrum.—A very remarkable confirmation, too, has been afforded to the doctrine of the constitution of the Spinal Cord here advocated by the Pathological researches of Dr. Ludwig Turck;* who has shown that certain lesions of the Encephalon produce a degeneration of nerve-tissue in particular tracts, which may be traced continuously down the Spinal Cord, usually in the *anterior* column of the side affected, and in the *lateral* column of the opposite side; whilst, on the other hand, local lesions of the Spinal Cord, as from caries of the vertebræ, or from the pressure of tumours, produce a like degeneration in certain tracts of the posterior columns, and sometimes also of the lateral columns, ascending towards the Encephalon. Thus it appears that the *posterior* fasciculi are liable to this secondary degeneration in the *centripetal* direction only, and the *anterior* in the *centrifugal* direction only; the degeneration taking place, in each case, in the direction in which they ordinarily transmit nerve-force. The mixed endowments of the *lateral* columns are also indicated by these phenomena; and Schiferdecker found that these fasciculi atrophied in the inferior or distal part of a divided Spinal Cord. Hence it seems to follow that their nutritive centre must lie in the cerebrum. The anterior roots of the spinal nerves have their nutritive centre in the grey matter of the Spinal Cord. The fasciculi *c* and *h* atrophy in the upper or proximal part of the Cord after its section; the latter probably have their nutritive centre in the ganglia of Clarke's column, and the former in the spinal ganglia of the posterior roots. Those fibres which do not atrophy after section of the Cord are probably commissural fibres from one part of the Cord to

* See his Memoir 'Ueber secondäre Erkrankung einzelner Rückensmarksstränge und ihrer Fortsetzungen zum Gehirne,' in "Denkschriften der Kaiserlichen Akademie der Wissenschaften," Wien, 1851; also "Zeitschrift der Gesell. der Aertze zu Wien," Band ix. Heft 10.

† The materials of this section have been chiefly taken from Landois, "Physiologie," 1880, pp. 702, 703.

another. The pyramidal fasciculi and the pyramids themselves are absent in cases of congenital absence of the brain.* In regard to the period of development of the several fasciculi, Flechsig states that the first to form are the nerve-roots, or the paths for nervous influence, extending between the periphery and the central grey substance of the Cord. Then those commissural fibres originate which connect different parts of the Cord with each other. Then those fibres which extend from the grey substance of the Cord to the cerebellum and to the tegmentum of the pedunculus cerebri; and, finally, those fibres which constitute a connection between the grey substance of the Cord and the pes of the pedunculus cerebri, and perhaps with the cortex of the brain itself.

442. The observations of Clarke show clearly that some of the fibres of the anterior roots never become longitudinal, and these, accordingly, have no other ganglionic centre than the vesicular substance of the segment of the Cord with which they come into immediate relation; they also render it extremely probable that many of the longitudinal fibres of both roots pass continuously upwards to the Encephalon, most of them after traversing the grey nucleus, but some of those of the posterior roots without even entering the vesicular substance, so that *these* cannot have their ganglionic centre in the Cord at all. If the latter be among the fibres which pass up through the Posterior Pyramids into the sensory tract of the Crura Cerebri, their true ganglionic centres are the Thalami Optici. That such is the real arrangement, is very strongly indicated by the analogous conformation of the gangliated cord of Arthropoda; for it may be stated with tolerable certainty, that some of the root-fibres of their nerves pass along the purely-fibrous tract of that cord (which is far more readily separated from the vesicular than it can be in Vertebrata) directly to the cephalic ganglia, which they thus bring into direct communication with all the nerve-trunks connected with the gangliated cord; but that others, also becoming longitudinal, and running along those portions of the cord which intervene between and connect the ganglia of the different segments, pass into the nerve-trunks that emerge from ganglia at a distance of one, two, three, or more segments above or below; whilst a large proportion of the root-fibres have their ganglionic centres in the ganglia which they respectively enter; and, after coming into relation with its vesicular substance, pass out again, either on the same or on the opposite side of the median plane.* Now the purely-fibrous tract of the ventral cord of the Arthropoda terminates in the Cephalic ganglia, which are homologous, as already remarked (§ 404, IV.), not with the whole Encephalon of Vertebrata, but with their 'sensory ganglia' alone; and thus analogy would lead us to suppose, that the fibrous strands of the Spinal Cord do *not* pass on continuously to the *Cerebrum*, but really extend no further upwards than the Corpora Striata, Thalami Optici, and the other ganglionic centres in connection with them which lie along the floor of the cranial cavity. This view will be hereafter shown (Sect. 3) to be in harmony with anatomical and physiological facts, which indicate that the Cerebrum only receives its impulses to action through the medium of the Sensory Ganglia, and that it reacts upon the muscular apparatus only through the same channel. That some of the afferent fibres of the spinal nerves should ascend continuously upwards to the ganglia of tactile sense, in Man and other Vertebrata, as well as in Arthropoda, would seem a legitimate deduction from the fact that such continuity obviously exists between the olfactory, visual, and auditory nerves, and *their* respective ganglionic

* See "Princ. of Comp. Phys.," § 648.—The important facts here referred to have been chiefly substantiated by the researches of Mr. Newport and M. Günther.

centres, no intermediate apparatus of vesicular matter being interposed in their course; and, as we have seen (§ 439), the existence of such a continuity in regard to a part of the fibres of the posterior roots of the nerves, is made extremely probable by the researches of J. L. Clarke.

443. We are not required, however, by the adoption of this view of the constitution of the Spinal Cord to regard its Cephalic fibres as of a *different order* from those which pass from one of its own segments to another; for, considering the whole of the Cranio-Spinal axis as *one series of centres*, receiving the terminations of all the nerves, its longitudinal fibres are equally *commissural*, whether they establish the connection between the nerve-roots and vesicular matter of two adjacent segments, or whether they bring into the same structural relation the parts which are furthest removed in position. And thus we may regard all impressions upon the afferent nerves as first operating upon it (affecting the consciousness, or not, according as they reach the Sensory Ganglia, or are arrested in their progress thither); and all motor impulses, whether purely-reflex, or originating in volitional direction or emotional excitement, as issuing immediately from it through the motor trunks.—If such be the case, it does not seem at all improbable that there should be a difference in different tribes of animals, as to the proportion of fibres which have their centres in the Spinal Cord and in the Sensorial centres respectively; for in those whose ordinary movements of progression, &c., are independent of sensation, being performed through the reflex action of the spinal cord, it might be expected that the chief connection of the spinal nerves should be with its own ganglionic substance, and that the bulk of the fibrous columns should be composed of commissural fibres resembling those which intervene between the separate portions of the ganglionic tract of the ventral cord of Arthropods; whilst in like manner it might be anticipated that in man, so large a portion of whose movements are performed in obedience to a mental stimulus and under the guidance of sensation, the longitudinal strands should be chiefly composed of fibres that directly connect the sensorial centres with the roots of the spinal nerves. Such a difference would appear, from the comparative researches of MM. Volkmann and Kölliker, to exist between the structure of the Spinal Cord of the Horse and that of Man.

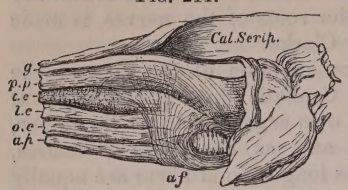
444. The *Medulla Oblongata*,* or cranial prolongation of the Spinal Cord, which brings it into connection with the Encephalic centres, is distinguished by the highly complex arrangement of its fibrous strands and of its nuclei of grey matter; and also by the peculiar distribution and endowments of the nerves connected with it. The anatomical boundaries usually assigned to it are the Pons Varolii above† and the Occipital foramen below; but these limits are purely artificial, and for physiological purposes the course of its fibres must be traced much higher. The part thus marked out has a bulb-like form, and presents, like the Cord of which it is the continuation, a posterior and an anterior median fissure. The former is deep and narrow at first, but suddenly widens out to form the space known as the *sinus rhomboidalis* or Fourth ventricle. The latter is wider and less deep; and its continuity with

* For good accounts of the anatomy of the Medulla Oblongata, see Dr. John Reid in "Edinb. Med. and Surg. Jour.," 1841; Mr L. Clarke in the "Phil. Trans.," 1858, vol. i., and 1868, Pt. i.; and Dr. John Dean, 8vo, 1863. Schröder v. d. Kolk, "Syd. Soc. Transl." Meynert, Art. 'Brain of Mammalia' in Stricker's "Hum. and Comp. Histology," Syd. Soc. Trans., vol. ii. 1872, p. 367. Henle, "Handbuch der Nervenlehre." Schwalbe, "Lehrbuch der Neurologie," 1880.

† From which it is separated laterally in animals by a broad band termed the Trapezium, but in man by a groove; the trapezium forming the posterior border of the Pons. See L. Clarke, "Proceed. Roy. Soc.," vol. xi. p. 360.

the anterior fissure of the Spinal Cord is interrupted by the decussation of the Anterior Pyramids, which is marked externally by the crossing of from three to five bundles of fibres from each side over to the other. This decussation may be considered as the physiological boundary between the Medulla Oblongata and the Spinal Cord. The surface of each lateral half is furrowed by grooves, which assist in marking out the several strands of nerve fibres that may be distinguished on either side. The vesicular substance is aggregated into several pairs of ganglionic nuclei which form extremely important nerve centres. The principal columns of the Medulla Oblongata on each side are—

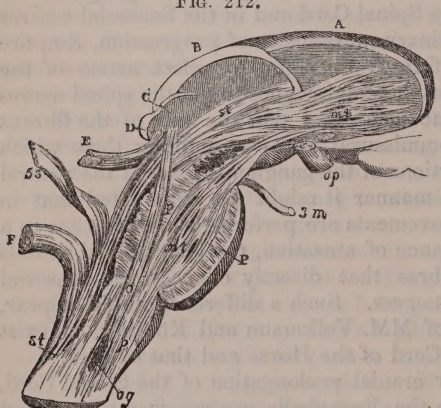
Fig. 211.



Lateral view of the *Medulla Oblongata*:—*a p*, anterior pyramid; *o c*, olivary column; *l c*, lateral column; *t c*, tubercle of Rolando, or tuberculum-cinereum; *c r*, corpus restiforme; *f*, *g*, fascicular gracilis; *a*, *f*, arciform fibres; *Cal. Scrip.*, calamus scriptorius. Between *f g* and *p x* is the sulcus intermedius posterior; between *a p*, and *o c* is the sulcus intermedius anterior.

445. The *Anterior Pyramid*, or Funiculus Pyramidalis, which consists entirely of fibres, establishing a communication between the 'motor tract' (Fig. 212, *m t*) of the Crura Cerebri, and the anterior and antero-lateral columns of the Spinal Cord. Some of the fibres of this column are derived from the anterior column of the cord of their own side, others are derived from the anterior column of the opposite side, but by far the largest number are a continuation upwards of the fibres running in the posterior part of the lateral column of the opposite half of the cord, and their decussation is very apparent at the lower and front part of the Medulla Oblongata.* Some fibres have been traced by Clarke† into the posterior columns and posterior cornu of the cord. On reaching the pons, the anterior pyramids are concealed by the transverse fibres of that body, but may be traced into the peduncles of the cerebrum.—The *Olivary Funiculus* is composed of white fibres, and presents at its upper and median part a swelling named the *olive*, which encloses a large grey motor nucleus (Fig. 212, *o g*). The upward continuation of this funiculus divides, while passing through the Pons Varolii, into two bands, one of which proceeds upwards and forwards as a part of the 'motor tract' (*m t*) of the Crus Cerebri, whilst the other (*o*) proceeds upwards and backwards to reach the Corpora Quadrigemina (c, d). The Olivary columns are continuous inferiorly with the antero-lateral columns of the Spinal Cord. The vesicular nucleus of the *olive*, which is known as the '*Corpus dentatum*,' and which appears first amongst the network of fibres into which the anterior cornu is resolved, and the outer portion of the anterior column, seems to be intimately connected

Fig. 212.



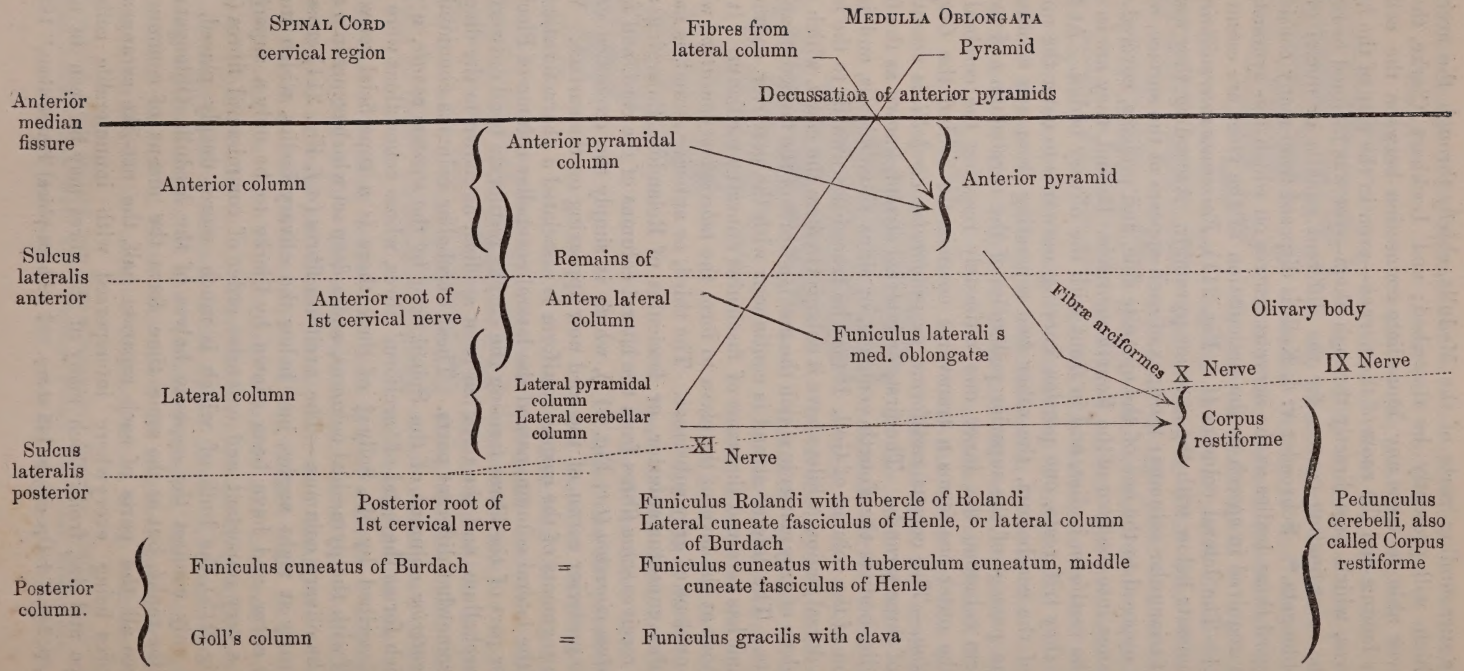
Dissection of the *Medulla Oblongata*, to show the connections of its several strands:—A, corpus striatum; B, thalamus opticus; C, D, corpora quadrigemina; E, commissure connecting them with the cerebellum; F, corpora restiformia; P, P, pons Varolii: *s t*, *s t*, sensory tract, *m t*, *m t*, motor tract; *g*, olivary tract; *p*, pyramidal tract; *o*, *g*, olivary ganglion; *o p*, optic nerve; 3 *m*, root of the third pair (motor); 5 *s*, sensory root of the fifth pair.

* Rosenthal, "Ein Beitrag zur Encephalotomie," Weimar, 1815. Reid, "Edinb. Med. and Surg. Journ.," Jan. 1841; and "Physiol., Pathol., and Anat. Researches," chap. vii.

† "Phil. Trans.," 1858, p. 238. See also Meynert, op. cit., p. 528.

with all the surrounding parts of the Medulla, chiefly through the arciform system, which will presently be described; and Lockhart Clarke, though he was never able to trace any immediate connection between the cells of the nuclear laminæ and the roots of the nerves—even in the case of the hypoglossal nerves, which pass directly through them—yet was inclined to regard them as the co-ordinating centres for the different ganglia or nuclei of the Medulla Oblongata.* Schroeder v. d. Kolk is disposed from many considerations to regard these bodies as the nervous centres on which the symmetrical movements required in speech or the articulation of the voice are essentially dependent.†—The lateral columns (*l c*, Fig. 211), *Faisceaux intermédiaires* of Longet, decussate below with the anterior pyramids. Ascending, they assume the form of triangular columns; the apex of each appears at the surface, whilst the base is opposed to the one of the opposite side, and projects, covered with grey substance, into the floor of the Fourth ventricle. Behind, they are in contact with the restiform bodies, and in front with the olivary bodies. At their upper end they trifurcate, one portion curving outwards to enter the middle peduncle of the cerebellum, the other two separating from one another to allow of the passage of the superior peduncles of the cerebellum and part of the restiform columns, the inner one ultimately reaching the cerebral peduncles; the outer one forms a transverse commissure behind the *Corpora Quadrigemina*.—The corpus restiforme, or *pedunculus cerebelli*, is essentially composed of three strands. The first, or internal strand, known as the fasciculus gracilis, bounds the Fourth ventricle, or sinus rhomboidalis, and is the continuation of the column of Goll. It may be traced downwards to the lower part of the dorsal region, whilst above it enlarges to form the *clava*, which contains a nucleus of grey matter in which the median fibres of the fasciculus appear to terminate. The lateral strand is continuous with the posterior column of the cord, and has received the name of fasciculus cuneatus medianus. It also enlarges above at the level of the clava to form the *tuberculum cuneatum*, which contains a nucleus of grey substance. The third, or anterior strand, is named the fasciculus cuneatus anterior, or fasciculus of Rolando. Enlarging as it ascends, it receives some fibres from the lateral columns of the cord, and forms the *tuberculum cinereum* (*t c*, Fig. 211), which is simply the expanded extremity of the posterior cornu of the cord now appearing on the surface. With these three segments of the corpus restiform is associated a characteristic constituent of the lateral column, named the lateral cerebellar column of Flechsig. The greater part of the fibres forming the corpus restiforme bend outwards to enter the cerebellum, and the term has been applied, as shown in the diagram p. 376, to somewhat different parts. These Cerebellar columns communicate with the *anterior* columns of the Spinal Cord by the *stratum zonale*, a portion of which forms the band of 'arciform' fibres, whose connections were first distinctly described by Mr. Solly;‡ of these there is a superficial set which unites itself with the pyramidal columns, and a deep set which comes into relation with the olivary columns.—The arciform fibres (*a f*, Fig. 211) cross the Medulla nearly at right angles, just below the olivary bodies, which indeed they partly cover, and have been shown by Clarke to be only a superficial portion of a very important and extensive order of commissural fibres (well seen in Fig. 215), the bulk of which is much more deeply placed, and which not only connect the opposite halves of the Medulla Oblongata by traversing the raphé, but at the same time form the means of communication between all the parts of each separate half, the net-like arrangement of the fibres being everywhere interspersed with innumerable cells of varied shape and size, from which many of the fibres may be seen to arise.

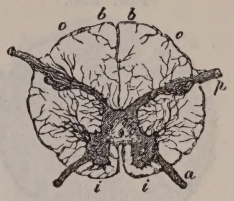
* Op. cit., p. 245. † Op. cit., p. 148 *et seq.* ‡ "Philosophical Transactions," 1836.



Structural Relations of Spinal Cord to Medulla Oblongata.

The gradual development of the several centres of grey substance in the Medulla Oblongata, and the relations which they bear to the Cerebral nerves, most of which take their origin from this part of the Spinal axis, may be rendered intelligible by a comparison of the following diagrams. The first section here shown (Fig. 213) is made at the level of the lower fibres of origin of the first Spinal nerves. On comparing the shape and position of the grey substance with its appearance, as shown in Fig. 207, it will be observed that the whole of the grey substance is here placed more anteriorly than in that section; that the posterior white columns (*o* and *b*) are of large size, whilst the anterior and antero-lateral columns are comparatively small. In Fig. 214 the grey substance is seen to have relatively increased in size, but to have become somewhat broken up. On each side of the posterior median fissure a remarkable longitudinal column (*b*), containing grey matter in its interior, termed the 'pyramidal column,' is beginning to appear; a second swelling, situated on the Cervix a little more externally to that just mentioned, indicates the commencing appearance of the restiform nucleus of Clarke; still more externally, the Caput Cornu may be seen to be detached and thrown aside from the rest as a distinct mass, which is traversed successively by the vagus and glosso-pharyngeal nerves, and then becomes the principal nucleus of the sensory root of the 5th pair. The decussation of fibres proceeding from the deeper part of the lateral column (between *p* and *a*, Fig. 213) to form the anterior columns is also here well seen, and the central grey substance has re-assumed a triangular form. In the next section (Fig. 215), made about $\frac{1}{4}$ of an inch below the olivary bodies, the grey matter of the posterior pyramids (*b*) on either side of the posterior median fissure is seen to have considerably increased in size; the slight swelling at the base of the Cervix is also now much larger, and has become the grey nucleus of the restiform bodies (*o*), whilst what was the Caput Cornu is pushed still further forwards, and forms a great mass of grey matter at the side of the cord known as the Grey Tubercle of Rolando (*e*, Figs. 216, 217). The commissural direction and arrangement of the fibres of the anterior pyramids are also still apparent. They come principally from the central grey substance, and scarcely at all from the lateral columns. On making a section just below the olivary bodies (Fig. 216), the grey matter is found to occupy almost the whole of the posterior pyramids (*b*), and a large portion of the restiform bodies (*o*), whilst a most delicate and complex system of interlacing fibres surrounds the central canal. The grey tubercle of Rolando having increased in size and reached the surface of the Medulla, appears as a dark streak (*t c*, Fig. 211); the portion of the anterior column which does not decussate has been left white on the right side of this drawing. Two minute

Fig. 213.

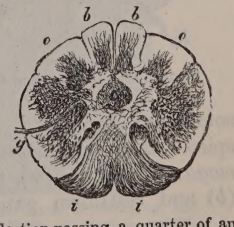


Section made opposite First pair of Cervical Nerves.—The following references indicate the same parts in Figs. 216–219:—*a*, anterior, *p*, posterior root of Spinal Nerve; *i*, *i*, anterior white column; *o*, posterior white column below, but in the higher sections restiform body; *b b*, posterior pyramids; *e*, grey Tubercle of Rolando; *Hg*, Hypoglossal Nerve; *Sp. Ac.* Spinal Accessory Nerve; *V*, Pneumogastric Nerve; *gp*. Glosso-pharyngeal Nerve.

Fig. 214.

Section passing through upper fibres of origin of First pair of cervical Nerves.

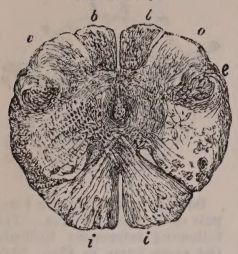
Fig. 215.



Section passing a quarter of an inch below Olivary bodies.

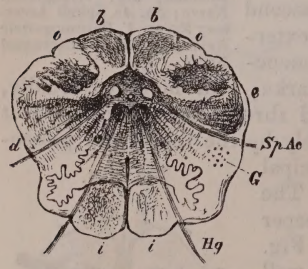
dark spots may be noticed near the bottom of the posterior fissure; these are imbedded in the mass of cells forming the chief ganglionic centres of the spinal accessory nerve, though other and extremely fine rootlets belonging to these nerves may be traced arising from the lateral grey substance and base of the anterior cornu of the spinal cord or tractus intermedio-lateralis, and issuing with the posterior roots of the Spinal nerves as low down as the sixth or seventh cervical vertebra. Fig. 217 is taken from a section made through the lower part of the Olivary body. The posterior pyramids (*b*) still contain much grey matter, and the restiform nucleus and grey tubercle of Rolando are strongly defined. The small central canal has become closely approximated to the bottom of the posterior median fissure, and on either side of it are the ganglionic masses from which the spinal accessory nerve takes its origin, whilst immediately in front of it are two dark spots containing large multipolar cells indicating the ganglia of origin of the hypoglossal nerve, other fibres of which last, like those of the spinal accessory nerve, may be traced downwards, and arise from the upper remains of the anterior cornu, whilst a few of the superior fibres cross the raphé. Anteriorly the windings of the corpus dentatum or olivary nucleus are visible, with a remarkable set of ganglionic cells indicated by G, constituting the vaso-motor centre,* and termed the *antero-lateral* nucleus. These are connected together by a network in the lateral column, and by nerve fibres from the Tubercle of Rolando. The whole central part of the grey substance of the Medulla is shown to be composed of commissural bundles constituting the deep system of arciform fibres described by Lockhart Clarke. The decussation of the anterior pyramids is here much diminished; for the fibres they derive from the lateral columns, which at first were their principal source, have become comparatively few; whilst those that proceed from the posterior columns and central grey substance have been gradually increasing in number, though not in a corresponding proportion. The section shown in Fig. 218 is carried through the Medulla just at the point of the Calamus Scriptorius, and shows that the hypoglossal ganglia have retreated somewhat backward, pushing the mass of ganglionic cells from which the spinal accessory arose, but which now constitute the origin of the *Pneumogastric Nerves* (v), to some extent outwards.† The posterior pyramidal (*b*) and restiform ganglia (*a*) have increased in size, and by their lateral

Fig. 216.



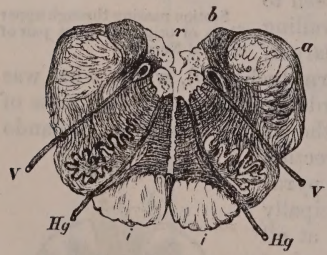
Section immediately below Olivary bodies.

Fig. 217.



Section through lower part of Olivary body.

Fig. 218.



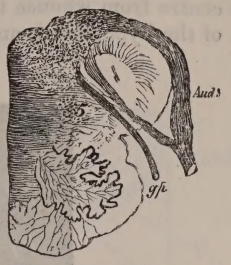
Section through point of Calamus Scriptorius.

* Dittmar, Ludwig's "Arbeiten," 1873, p. 115.

† The vesicular column which gives origin to the fibres of the spinal accessory, becomes the centre for the Vagus about the level of the middle of the olivary bodies. Lockhart Clarke, "Phil. Trans.," 1868 Pt. i. p. 283

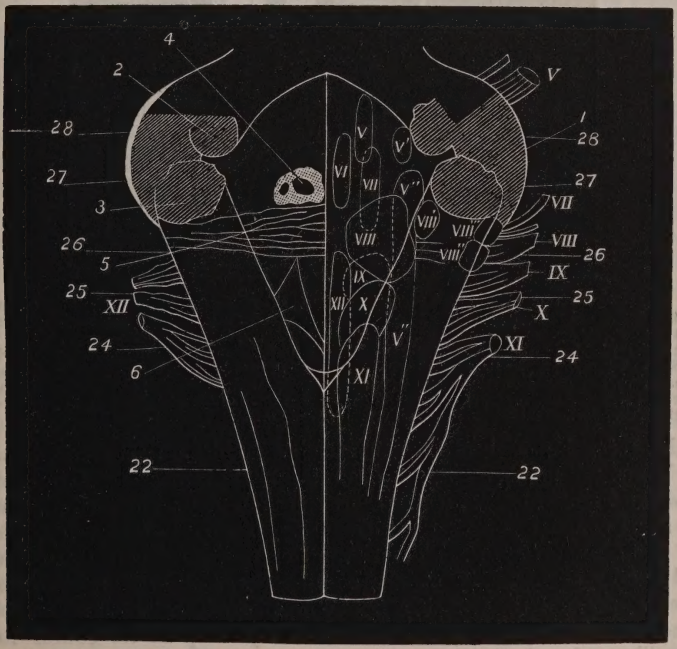
expansion form nearly one continuous mass on each side of the Medulla, which, from the close interlacement of their fibres, presents a spongy appearance, numerous cells being contained in the interstices. The section displayed in Fig. 219 is carried through the upper part of the Medulla Oblongata, and shows the Glosso-Pharyngeal arising at a higher level, but from the same series of ganglionic cells as those from which the Spinal Accessory and Pneumogastric roots have successively arisen, and which are now sunk between two new masses of vesicular substance from which the Auditory nerves take their origin. The Auditory nerve itself is seen to divide into two portions, one curving round the side of the Medulla, and forming the well-known transverse elevation on the floor of the Fourth Ventricle, to terminate in the inner or posterior auditory nucleus and to some extent in the outer nucleus, the other dipping into the substance of the cord in front of the Restiform body to reach the outer nucleus formed by the summit of the posterior pyramid, and apparently by part of the nucleus of the Pneumogastric nerve. The ganglionic cells which give origin to the motor and sensory roots of the 5th nerve are here very apparent. The position of the several nuclei of origin of the different cerebral nerves may be understood from a study of the two accompanying woodcuts.

Fig. 219.



Section through upper part of the Medulla Oblongata.

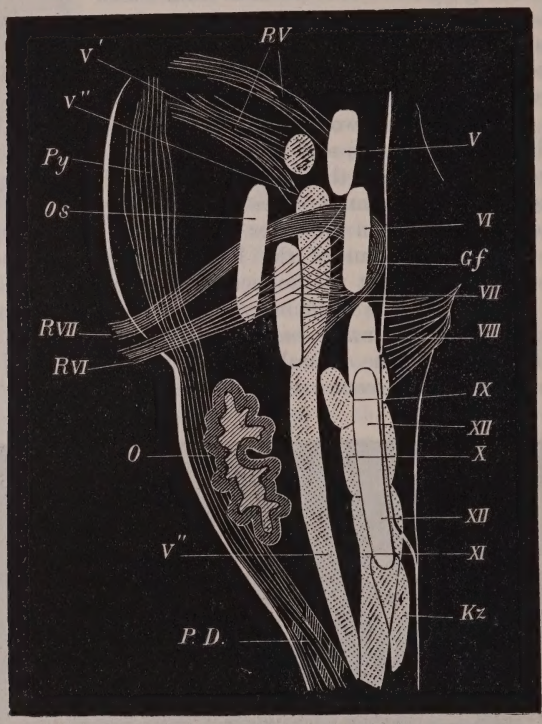
Fig. 220.



Transparent view of the Medulla from behind. The position of the nerve nuclei is shown on the right hand, and numbered with Roman numerals:—V, Motor nucleus of the Fifth; V′, median, and V″, sensory nucleus of the Fifth; VI, nucleus of the Sixth nerve; VII, facial nucleus; VIII, posterior median nucleus of the auditory nerve; VIII′, anterior median; VIII″, posterior, and VIII‴, anterior lateral auditory nucleus; IX, glosso-pharyngeal nucleus; X, nucleus of vagus; XI, nucleus of Accessorius; XII, nucleus of Hypoglossal; 1, crus cerebelli ad pontem; 2, crus cerebelli ad corpora quadrigemina; 3, crus cerebelli ad medullam; 4, eminentia teres; 5, striæ acusticæ; 6, ala cinerea. The Roman numerals V—XII, indicate the corresponding nerve roots 22—28, section of nerve roots.

The deep origins of the 5th, 6th, and Portio Dura of the 7th, are further shown in the section Fig. 222. The 6th and Portio Dura seem to form almost a loop, and to be continuous with each other through a common ganglionic centre from whence they arise, situated above but in the same line with that of the hypoglossal, and both may be traced to a grey mass in front of the

Fig. 221.



Transparent lateral view of the Medulla, showing the relative positions of the most important nuclei; right half of the medulla seen from the surface of the section; Py, pyramidal tract; P, D, decussation of pyramids; O, olivary body; O s, superior olivary body; V, motor; V′, middle sensory; V″, inferior sensory nucleus of the Fifth; VI, nucleus of the Sixth; G f, genu of the Facial; VII, nucleus of the Facial; VIII, posterior median auditory nucleus; IX, glosso-pharyngeal nucleus; X, nucleus of vagus; XI, nucleus of spinal accessory; XII, nucleus of hypoglossal; K z, nucleus of the funiculus gracilis; Rv, roots of the Fifth; Rvi, of the Sixth, and Rvii, of the Facial nerves.

fasciculus teres, but each of these nerves has besides a separate nucleus of its own. When the portio dura of the seventh nerve reaches the fasciculus teres, as shown in Figs. 221, 222, it runs longitudinally down the medulla, and after a very short course again bends transversely *forward* to form a loop along the side of the median furrow. The summit of this curve constitutes the longitudinal bundle of fibres, of which the upper end is seen in sections made just below the fourth ventricle. The loop encloses the nucleus common to it and the sixth, and the lower arm of the loop in its course forwards divides like a brush into separate fibres, which plunge into the motor nucleus of the fifth nerve, and into the superior olivary body, or grey nucleus of the trapezium. As regards the 6th, the lower fibres arise from the ganglion common to it and the portio dura of the 7th, and also from the grey matter of the fasciculus teres, whilst the upper fibres arise from the

upper and inner part of the common ganglion, which may here be regarded as a separate centre or nucleus, as the outer portion, from which the portio dura previously arose, has become much attenuated, and ceases to give origin to the fibres of that nerve. The roots of origin of the 6th pair do not decussate. The close relation which exists between the nuclei of origin of the hypoglossal, glosso-pharyngeal, spinal accessory, vagus, facial, and trigeminal nerves, is of much interest, and serves to explain certain symptoms accompanying various forms of paralysis, in which the muscles concerned in deglutition, vocalization, articulation, and expression are affected. The motor and sensory roots of the 5th are separated from one another at their origin by the Portio Dura. The connection of the motor root with the glosso-pharyngeal nucleus and with the fasciculus teres or nucleus of the 7th, has already been noticed. The Posterior or Sensory root runs down through the front of the grey tubercle or caput cornu posterior, which may be regarded as the continuation of its nucleus, and is in most intimate relation with the fibres of origin of the vagus and glosso-pharyngeal nerves, which pass this portion of the fifth nerve. The origins of the 4th pair of Cerebral nerves have been ascertained to be traceable on either side through the thin lamina constituting the valve of Vieussens, and through the columns forming the lateral boundaries of the Aqueduct of Sylvius, to near the floor of the fourth ventricle;* whilst the third nerve, the apparent origin of which is from the *locus niger* of the Cerebral peduncles, has been followed by Stilling to a grey nucleus underlying the Aqueduct of Sylvius, and has been shown by Clarke to be in close relation with the grey tubercle into which the sensory root of the 5th penetrates, and the nucleus common to the portio dura and abducens nerves. In order to complete the descriptions of the origins of the Cerebral nerves, it is only requisite here to mention that the 2nd pair, or Optic nerves, arise from the posterior part of the Optic thalami and from the Corpora Quadrigemina; whilst the 1st pair, or Olfactory nerves, arise by three roots, the outer one appearing to be connected with the Corpus Striatum of its own side, the inner one with the Lamina Cinerea in front of the Optic commissure, and the middle one springing from a grey nucleus in front of the anterior perforated space.—It will thus be seen that the whole series of the Cephalic nerves, when followed to their origin, arise from grey ganglionic centres situated along the floor of, or just below, the fourth ventricle and the base of the brain. These, there can be little doubt, are more or less intimately connected with one another by longitudinal and transverse commissural fibres, and establish the existence of a Sensory tract, the activity of

FIG. 222.

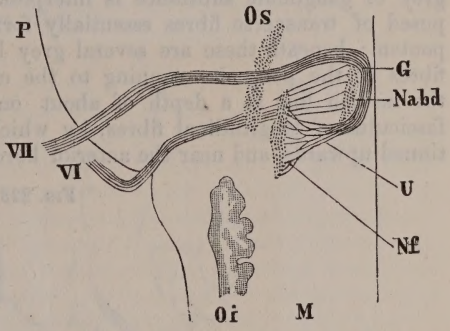


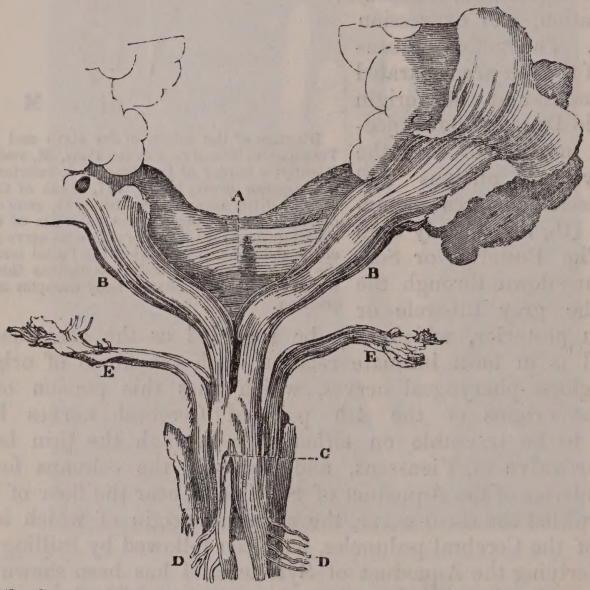
Diagram of the origin of the sixth and Facial Nerves. Transparent lateral view of the Pons. M, medulla oblongata, P, anterior border of the Pons; O i, inferior olivary body; O s, superior olivary body; VII, trunk of the Portio dura raised a little to avoid confusion; G, genu of the intermediate portion; U, deep fibres of origin of the Facial; Nf, Facial nucleus; VI, sixth or abducens nerve; Nabd, nucleus of the abducens. In this view the Facial nucleus is nearest the observer, and the abducens nucleus the most distant, whilst the superior olivary body occupies an intermediate position.

* See Duval, Robin's "Journal de l'Anatomie," 1878, p. 456, who finds that in the cat the root fibres decussate in part.

which is of fundamental importance, as will hereafter be shown, in the origination of ideas and of a certain class of movements which may be termed 'consensual' or 'sensori-motor.'

The Pons Varolii is composed of numerous layers of white matter partly running longitudinally, partly transversely, between which some grey or ganglionic substance is interposed. The superficial layer is composed of transverse fibres essentially forming the processus e cerebello ad pontem; beneath these are several grey laminæ traversed by a deep set of fibres of the pons also running to the crura cerebelli. On each side of the median line at a depth of about one-sixth of an inch is a compact fasciculus of longitudinal fibres, by which the anterior pyramids are continued upwards, and near the anterior border of the pons diverge to enter the

Fig. 223.



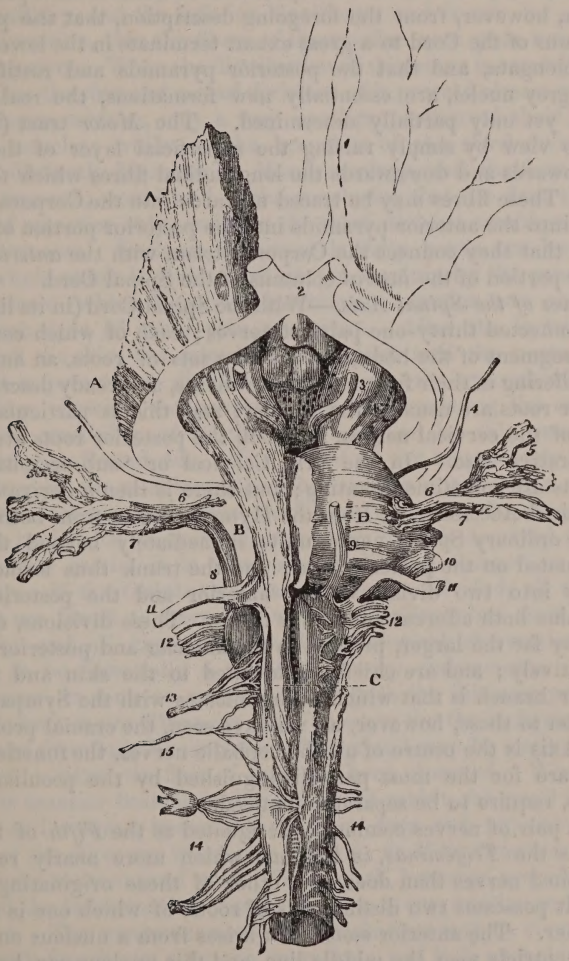
Course of the *Sensory tract* according to Sir C. Bell:—A, Pons Varolii; B, B, sensory tract separated; C, union of posterior columns; D, D, posterior roots of spinal nerves; E, sensory roots of fifth pair.

cerebral peduncles. Behind these and interlacing with their posterior portion are numerous small masses of grey matter, the *nuclei pontis*. These are succeeded at a greater depth by longitudinal fibres running downwards from the posterior part of the cerebral peduncle. Behind these fibres is the small superior olivary body. The posterior surface of the pons is composed of two pairs of flat longitudinal fasciculi, which are the continuation of the columns of the medulla oblongata. The median pair is the continuation of the fasciculi teretes, which form a projection on the floor of the fourth ventricle and pass upwards to the corpora quadrigemina; the lateral pair (lemniscus) is the continuation of the posterior and lateral columns of the medulla oblongata lying between the olivary body and restiform column.* They ascend on each side to the nates. The transverse fibres of the pons constitute the great commissure of the Cerebellum; and are an extension of the arciform fibres of the medulla oblongata; it will be observed that these fibres not only *surround* the longitudinal bands which

* German, äusseren Halsenstranges.

connect the Cerebral mass with the Spinal Cord, but *pass through* them so as in some degree to isolate the two lateral halves from one another, and to form a complete septum between the anterior and posterior portions of each. These *anterior* and *posterior* tracts of the Crura Cerebri are probably essentially subservient to the *motor* and *sensory* functions. The cells of the grey substance

Fig. 224.



Course of the *Motor tract*, according to Sir C. Bell;—A, A, fibres of the Hemisphere, converging to form the anterior portion of the crus cerebri; B, the same tract, where it passes the crus cerebri; C, the right Pyramidal body, a little above the point of decussation; D, the remaining part of the Pons Varolii, a portion having been dissected off to expose B.—1, olfactory nerve, in outline; 2, union of optic nerves; 3, 3, motor oculi; 4, 4, patheticus; 5, 5, trigeminus; 6, 6, its muscular division; 7, 7, its sensory root; 8, origin of sensory root from the posterior part of the medulla oblongata; 9, abducens oculi; 10, auditory nerve; 11, facial nerve; 12, eighth pair; 13, hypoglossal; 14, spinal nerves; 15, spinal accessory of right side, separated from par vagum and glosso-pharyngeal.

of the pons are generally round, oval, or fusiform, and of about the 1500th of an inch in diameter, and are so connected with nerve fibres in chains or bundles as to form a complete network, the principal chains of which have in general a longitudinal extension, and follow the course of the longitudinal

fasciculi of the anterior pyramids. The general relations of the Sensory tract were represented by Sir Charles Bell in the accompanying diagram (Fig. 223), in which the Medulla is opened on its posterior aspect, the restiform columns separated and turned aside so as to bring into view the posterior pyramids, some of the fibres of which may be traced upwards into the Thalami Optici, whilst they pass through the posterior pyramids into the posterior portion of the *lateral* columns, and also into the *posterior* columns of the Spinal Cord. It will be seen, however, from the foregoing description, that the posterior and lateral columns of the Cord to a great extent terminate in the lower part of the Medulla Oblongata, and that the posterior pyramids and restiform bodies, with their grey nuclei, are essentially new formations, the real function of which is as yet only partially determined. The *Motor* tract (Fig. 224) is brought into view by simply raising the superficial layer of the Pons, and following upwards and downwards the longitudinal fibres which there present themselves. These fibres may be traced upwards into the Corpora Striata, and downwards into the anterior pyramids into the posterior portion of the olivary columns, so that they connect the Corpora Striata with the *anterior*, and with the anterior portion of the *lateral* columns of the Spinal Cord.

446. *Nerves of the Spinal Axis.*—With the Spinal Cord (in its limited sense) there are connected thirty-one pairs of nerves; each of which corresponds to a vertebral segment of the body, and has two sets of roots, an anterior and a posterior, differing in their functional endowments, as already described (§ 418). The anterior roots are usually the smaller; and this is particularly the case with those of the cervical nerves, in which the posterior roots are of remarkable comparative size. In the first Cervical or 'sub-occipital' pair, the anterior roots are sometimes wanting; but there is then a derivation of fibres from the Spinal Accessory, or from the Hypoglossal, or from both. The two roots of the ordinary Spinal nerve unite immediately beyond the ganglion, which is situated on the posterior one; and the trunk thus formed separates immediately into two divisions,—the anterior and the posterior,—each of which contains both afferent and motor fibres. These divisions, of which the anterior is by far the larger, proceed to the anterior and posterior parts of the body respectively; and are chiefly distributed to the skin and the muscles. The anterior branch is that which communicates with the Sympathetic nerve. —In addition to these, however, as we have seen, the cranial prolongation of the Spinal Axis is the centre of all the cephalic nerves, the functions of which, since they are for the most part distinguished by the peculiarity of their endowments, require to be separately noticed.

447. The pair of nerves commonly designated as the *Fifth* of the Cephalic series, or as the *Trigeminus*, is the one which more nearly resembles the ordinary Spinal nerves than does any other of those originating within the cranium. It possesses two distinct sets of roots, of which one is much larger than the other. The anterior *motor* root arises from a nucleus on the floor of the fourth ventricle near the middle line, and this nucleus can be excited by the will through fibres proceeding from the opposite side of the encephalon. The *sensory* fibres arise from a nucleus (see Figs. 220, 221) in the pons; from the posterior cornu of the grey matter of the spinal cord as low down as to the middle of the cervical region; from a nucleus at the side of the aquæductus Sylvii, the fibres of which constitute the trophic root of Meckel; by decussating fibres from the substantia ferruginosa at the upper part of the fourth ventricle; and lastly, some fibres come from the pes of the peduncle of the cerebrum and some from the cerebellum. The fibres of origin of the sensory root communicate with the motor nuclei of every nerve arising from

the medulla oblongata, except the sixth,* which explains many of the reflex phenomena that are presented when the sensory fibres are stimulated. The larger root of the Fifth, like the posterior and larger root of the Spinal nerves, possesses a distinct ganglion, known as the 'Gasserian;' and the fibres of the smaller root, the number of which has been estimated at 9000 to 10,000, do not blend with those of the larger, until the latter have passed through this ganglion. The trunk of the nerve separates into three divisions,—the Ophthalmic, the Superior Maxillary, and the Inferior Maxillary; and it can be easily shown, by careful dissection, that the fibres of the smaller root pass into the last of these divisions alone. When the distribution of this nerve is carefully examined, it is found that the *first* and *second* divisions of it proceed almost entirely to the Skin and Mucous surfaces, only a very small proportion of their fibres being lost in the muscles; whilst of the branches of the *third* division, a large number are distinctly Muscular. Hence analogy, and the facts supplied by anatomical research, would lead to the conclusion that the first two divisions are nerves of sensation only, and that the third division combines sensory and motor endowments. Such an inference is fully borne out by experiment. When the whole trunk is divided within the cranium by the penetration of a sharp instrument (which Magendie, by frequent practice, was able to accomplish), evident signs of acute pain are given. After the incision has been made through the skin, the animal remains quiet until the nerve is touched; but when it is pressed or divided, doleful cries are uttered, which continue for some time, showing the painful effect of stimulating the cut extremity. The common sensibility of all the parts supplied by this nerve is entirely destroyed on the affected side. The jaw does not hang loosely, because it is partly kept up by the muscles of the other side; but it falls in a slight degree; and its movements are seen, when carefully observed, to be somewhat oblique. If the trunk be divided on each side, the whole head is deprived of sensibility; and the animal carries it in a curious vacillating manner, as if it were a foreign body.—If the *Ophthalmic* branch only be divided, all the parts supplied by it are found to have lost their sensibility; but their motions are unimpaired; and all experiments and pathological observations concur in showing it to be essentially a nerve of sensory endowments. A few motor fibres, however, in some animals pass directly to the dilatator pupillæ muscle, and in all secreto-motor fibres are distributed to the the lachrymal gland; by stimulation of these last the secretion of the gland may be excited, whilst after their section a paralytic flow of tears has been observed. When the whole nerve, or its anterior branch, is divided in the rabbit, the pupil is exceedingly contracted, and remains immovable; but in dogs and pigeons it is dilated. The pupil of the other eye is scarcely affected; or, if its dimensions be changed, it soon returns to its natural state. The eyeball, however, speedily becomes inflamed; and the inflammation usually runs on to suppuration and complete disorganization. The commencement of these changes may be commonly noticed within twenty-four hours after the operation; and it is probable they may in part be attributed to the want of the natural secretion, which is necessary to keep the mucous surface of the eye in its healthy condition, and partly to the loss of the sensibility of that surface leading to failure of the protective acts of winking; since, as Snellen† has shown, if the eye be carefully protected from the action of external and injurious agencies, no ill effects are observed. Pathological evidence, however, is not wanting to show that the fifth exerts some influence over the nutritive processes in the parts it supplies, which is probably

* Landois, "Lehrbuch der Physiologie," 1880, p. 667.

† "Ann. d'Oculist.," 1865, t. liii. p. 178.

transmitted through the vaso-motor nerves it contains.* The secretory activity of the lachrymal nerve may be reflectorially excited through the sensory branches of the fifth distributed to the conjunctiva and nose, through the olfactory and optic nerves, and indeed through the sensory branches of the cranial nerves generally.—The *Superior Maxillary* branch, considered in itself, is equally destitute of motor endowments with the ophthalmic; but its connection with other nerves, through the spheno-palatine ganglion, or rather its anastomosing twigs,† introduces vaso-motor fibres into it.—The *Inferior Maxillary* branch is the only one which possesses motor as well as sensory endowments in varying proportions, some being almost exclusively motor, and others as completely of a sensory character. The latter is probably the nature of the Lingual branch, the fibres of which present minute ganglia in the tongue, and there seems good reason to believe, as will hereafter be shown, that this ministers not only to the tactile sensibility of the tongue, but to the sense of Taste. The lingual nerves contain vaso-motor fibres. The muscles put in action by this division are solely those concerned in the masticatory movements.—The *Chorda Tympani*, though essentially destined to excite the sub-maxillary and sub-lingual glands to action, contains motor nerves, distributed to the muscles of the Tongue.‡ The 5th pair is connected, in different parts of its course, with a number of small ganglia belonging to the Sympathetic system. One of the most interesting of these ganglia is the *Ophthalmic* or *Ciliary* (Fig. 225, 29), which is the centre whence the eyeball derives its supply of nerves, sensory, motor, and sympathetic. The ganglion derives its sensory fibres by its 'long root' from the nasal branch of the Ophthalmic division of the 5th pair; its motor fibres, by the 'short root' from the 3rd pair; whilst by another small root it is connected with the cavernous plexus of the Sympathetic system,§ and is thus brought into relation with the Spinal

* See von Gräfe, "Archiv f. Ophthal.," 1854–55, p. 306; Longet, "Physiologie," 1861, vol. ii. p. 486.

† Since the ganglion has been shown by Prévost to be purely sensory. (Brown-Séquard's "Archives de Physiol.," 1868, pp. 7 and 207.)

‡ See Vulpian, "Gazette Hebdomadaire," 1873, No. 3.

§ The functions of this ganglion have been made the subject of particular investigation by Dr. C. Radclyffe Hall ("Edinb. Med. and Surg. Journal," 1846–48), whose most important results are as follows:—

1. The size of the ciliary ganglion is always in direct proportion to the activity of the iris, which in turn always bears a direct relation to the strength and acuteness of vision, and to the nocturnal habits of the animal, and implies a proportionate development of the internal vascular apparatus of the eye.

2. The ganglion is always more intimately connected with the 3rd pair than with any other; the size of the short root being always in direct relation to that of the ganglion, and the ganglion being sometimes a mere swelling on the trunk of the nerve.

3. The fibres derived from the 5th pair do not terminate in the ganglion, but pass onwards through it to the ciliary plexus.

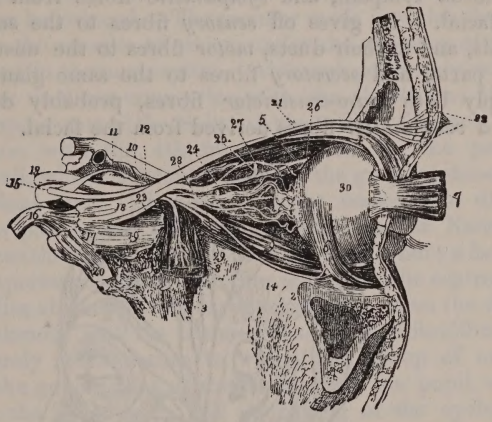
4. In the Rabbit, the iris receives fibres from the 6th pair which do not pass through the ganglion; and it is through this that the contraction of the pupil is produced in that animal by irritation of the 5th pair, which will not produce any effect upon the pupil of the Dog, Cat, or Pigeon, so long as it does not affect the brain to the extent of producing vertigo, nor affect the visual sense in any other way.

5. Irritation of the 5th nerve does not in any animal affect the action of the iris, *after* the division of the cerebral connections of all the other ocular nerves (this is denied by Budge), so that its influence over the movements of the iris must be reflected through the encephalic centres, not through the ophthalmic ganglion.

6. The function of the ganglionic centre itself, as a part of the Sympathetic system, seems to be to bring the 'organic actions' of the eyeball, especially its supply of blood, into harmony with its functional activity; this harmony being produced by the passage of the cerebro-spinal nerves through the ganglion, which excites the synergetic action of its own vesicles and nerve-fibres.—Irritation of the 3rd pair of nerves produces contraction of the pupil; irritation of the cervical portion of the Sympathetic, dilatation. On the other hand, paralysis

axis; for, according to Budge,* these fibres of origin for the Sympathetic nerve arise from two centres: first, from the Spinal Cord between the 6th cervical and the 2nd dorsal vertebra (a part which he terms the Centrum cilio-spinale inferius), the fibres from which pass upward in the great cord of the Sympathetic; and secondly, from another centre situated in the Medulla Oblongata, in immediate proximity to the origin of the Hypoglossal nerve, the fibres from this source passing into the superior cervical ganglion. The *sphenopalatine ganglion*, or ganglion of Meckel, is connected with the 2nd division

FIG. 225.



The *Nerves of the Orbit* seen from the outer side:—1, section of the frontal bone; immediately behind the numeral is the frontal sinus, and, in front, the integument. 2, the superior maxillary bone; the section in front of the numeral exhibits the maxillary sinus. 3, part of the sphenoid bone. 4, the levator palpebræ and superior rectus muscles. 5, the superior oblique muscle. 6, the inferior oblique muscle. 7, the ocular half of the external rectus muscle drawn forwards. 8, the orbital half of the external rectus muscle turned downwards. On this muscle the sixth nerve is seen dividing into branches. 9, the inferior rectus muscle. 10, the optic nerve. 11, the internal carotid artery emerging from the cavernous sinus. 12, the ophthalmic artery. 13, the third nerve. 14, the branch of the third nerve to the inferior oblique muscle. Between this and the sixth nerve 8 is seen the branch which supplies the inferior rectus; its branch to the ophthalmic ganglion is seen proceeding from the upper side of the trunk of the nerve, at the bottom of the orbit. 15, the fourth nerve. 16, the trunk of the fifth nerve. 17, the Gasserian ganglion. 18, the ophthalmic nerve. 19, the superior maxillary nerve. 20, the inferior maxillary nerve. 21, the frontal nerve. 22, its division into branches to supply the integument of the forehead. 23, the lachrymal nerve. 24, the nasal nerve; the small nerve seen in the bifurcation of the nasal and frontal nerve, is one of the branches of the upper division of the third nerve. 25, the nasal nerve passing over the internal rectus muscle to the anterior ethmoidal foramen. 26, the infra-trochlear nerve. 27, a long ciliary branch of the nasal; another long ciliary branch is seen proceeding from the lower aspect of the nerve. 28, the long root of the ophthalmic ganglion, proceeding from the nasal nerve, and receiving the sympathetic root which joins it at an acute angle. 29, the ophthalmic ganglion, giving off from its fore-part the short ciliary nerves. 30, the globe of the eye.

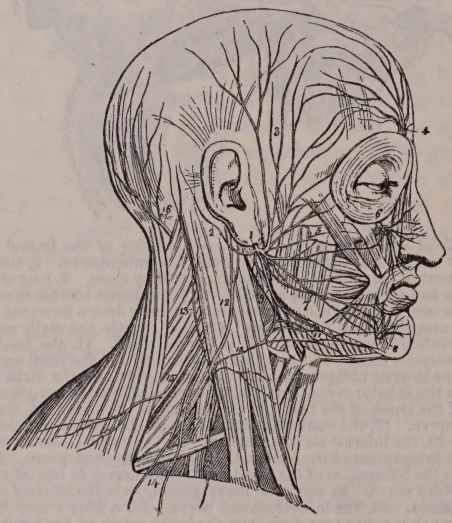
of the 5th as it traverses the sphenopalatine fossa. It receives *sensory* fibres from the superior maxillary division of the 5th, *motor* fibres from the Facial through the nervus petrosus superficialis major, and *sympathetic* fibres from the sympathetic plexus surrounding the carotid artery through the nervus petrosus profundus major. It supplies *motor* branches to the levator palati and azygos uvulæ muscles; *sensory* to the Schneiderian mucous membrane and forepart of the palate, stimulation of which induces sneezing; and probably *vaso-motor* and secretory branches to the same region. The *otic ganglion* is connected with the inner part of the 3rd division of the 5th, just after its exit from the skull. It receives *motor* branches from the inferior maxillary division of the 5th, and from the Facial through the nervus petrosus superficialis minor;

of the 3rd nerve is followed by dilatation; paralysis of the cervical sympathetic (as by section), by contraction of the pupil.

* "Physiologie," 1862, p. 767.

sensory fibres from the auriculo-temporal and from the glosso-pharyngeal nerves through the nervus petrosus superficialis minor; and vaso-motor fibres from the sympathetic plexus surrounding the middle meningeal artery. It supplies *motor* branches to the tensor tympani and tensor palati, and, by its connection with the auriculo-temporal and facial nerves, influences the *secretion* of the Parotid gland. The *submaxillary ganglion* is connected with the lingual nerve after it has been joined by the chorda tympani, and whilst it is lying on the hyoglossus. It receives *sensory* fibres from the lingualis; *motor* from the facial through the chorda tympani; *secretory* through the chorda tympani, and *sympathetic* fibres from the plexus surrounding the facial. It gives off *sensory* fibres to the submaxillary and sublingual glands, and to their ducts, *motor* fibres to the unstriated muscular tissue of these parts, and *secretory* fibres to the same glands; and it also appears to supply both *vaso-constrictor* fibres, probably derived from the sympathetic, and *vaso-dilator* fibres derived from the facial.

FIG. 226.



The distribution of the *Facial Nerve*, and the branches of the Cervical plexus :—1, the facial nerve, escaping from the stylo-mastoid foramen, and crossing the ramus of the lower jaw; the parotid gland has been removed in order to show the nerve more distinctly. 2, the posterior auricular branch; the digastric and stylo-mastoid filaments are seen near the origin of this branch. 3, temporal branches, communicating with (4) the branches of the frontal nerve. 5, facial branches, communicating with (6) the infra-orbital nerve. 7, facial branches, communicating with (8) the mental nerve. 9, cervico-facial branches, communicating with (10) the superficialis colli nerve, and forming a plexus (11) over the submaxillary gland. The distribution of the branches of the facial in a radiating direction over the side of the face, constitutes the pes anserinus. 12, the auricularis magnus nerve, one of the ascending branches of the cervical plexus. 13, the occipitalis minor, ascending along the posterior border of the sterno-mastoid muscle. 14, the superficial and deep descending branches of the cervical plexus. 15, the spinal accessory nerve, giving-off a branch to the external surface of the trapezius muscle. 16, the occipitalis major nerve, the posterior branch of the second cervical nerve.

448. The *Third*, *Fourth*, and *Sixth* pairs, together make up the apparatus of motor nerves, by which the muscles of the Orbit are called into action. The 3rd pair, or *oculo-motorius*, supplies the levator palpebræ, the superior, inferior, and internal recti; the circular fibres of the iris and the ciliary muscle, or Tensor choroideæ. Section or paralysis of the 3rd occasions drooping of the upper eyelid (ptosis); inability to move the eyeball in any direction except

outwards, and downwards and outwards, hence external strabismus; persistent dilatation of the pupil, and, owing to paralysis of the ciliary muscle, loss of accommodation of the eye for near objects. The 4th nerve is confined to the Superior Oblique, and the 6th to the External Rectus. The number of fibres in the 3rd nerve is about 15,000, in the 4th about 1100, in the 6th from 2000 to 2500.* The third and fourth nerves present some traces of sensibility, which in the former nerve is probably derived from the 5th. Chauveau† observes that the deep or intra-cerebral portions of the motor nerves are quite incapable of being excited to action by direct stimulation; though on applying irritation to them at the point where they emerge from the cerebrum, movements can always be induced.—The peculiar mode in which those motor nerves ordinarily excite the muscles to action, under the guidance of the visual sense, will be considered in the next section. Although commonly ranked as cephalic nerves, they have no direct connection with the Cerebrum; their real origin being from the upper part of the Spinal Axis. Thus the roots of the 3rd pair arise in common with the 4th from a nucleus in the pons beneath the Aqueductus Sylvii, which is a continuation of the grey substance of the anterior cornu of the spinal cord. They may also be traced into direct connection with the anterior pair of the Corpora Quadrigemina, or Nates, and with the Lenticular nucleus through the Peduncle of the Cerebrum; a fact of considerable physiological importance, as will hereafter appear. The centre for accommodation of the eye lies above the corpora mammillaria, when the floor of the third ventricle is continuous with the posterior wall of the infundibulum.—The chief actions of a purely *reflex* nature to which this group of nerves ordinarily ministers, are the government of the diameter of the pupil, which is accomplished through the Third pair; and the rolling of the eyeball beneath the upper lid during sleep, as well as in the efforts of sneezing, coughing, &c. But irregular movements of the eyeballs, which must be referred to the same group, are continually seen to accompany various abnormal forms of convulsive action.

449. The Portio Dura of the 7th pair, or Facial Nerve, containing about 4000 to 4500 nerve-fibres, was shown by Bell to be a motor nerve, chiefly distributed to the muscles of the face; it has hence been termed the Nerve of expression. In its passage through the Aqueductus Fallopii, it presents a gangliform enlargement, which is connected by the nervus petrosus superficialis major with the spheno-palatine ganglion of the 5th, and by the nervus petrosus superficialis minor with the otic ganglion.—By these branches the palatine muscles supplied by these ganglia receive their motor power, and some sensory fibres enter the facial, thus accounting for its sensibility when cut at its exit from that canal. It is also connected with the tympanic nerve of Jacobson proceeding from the glosso-pharyngeal, with the auricular of the pneumogastric, and with the upper cervical nerves. The Portio Dura, besides the muscles of the face, supplies the stapedius, the auricular, occipital, stylo-hyoid, and the posterior belly of the digastric muscles. It does *not* supply the muscles of mastication. Its chorda tympani branch joins the lingual of the fifth, and has been shown by Bernard to be the nerve by which the vessels supplying the submaxillary and sublingual glands can be caused to dilate, and both glands excited to active secretion, while other branches minister to taste, and supply the lingualis muscle.—Experimental as well as anatomical researches leave no doubt that the Portio Dura is the *general motor* nerve of the face; ministering to the influence of Volition and of Emotion, and also being the

* Rosenthal, "De Numero atque Mensura Microscop. Fibrillarum," Breslau, 1845.

† "Journal de la Physiologie," tom. v., 1862, p. 272.

channel of the reflex movements concerned in respiration, as of other automatic actions of the muscles.

450. Although the functions of the *Glosso-Pharyngeal* nerve have been heretofore alluded to in part, several questions still remain to be discussed in regard to them. Reasons have been given for the belief that it is chiefly an afferent nerve,—scarcely having any *direct* power of exciting muscular contraction, but conveying impressions to the Medulla Oblongata, which produce *reflex* movements of the motor nerves concerned in deglutition (§ 91).* This view of its function was deduced by Dr. J. Reid from minute anatomical investigation, and from a large number of experiments. Some experimenters assert that they have succeeded in exciting *direct* muscular actions through its trunk; but these actions seem to be limited to the stylo-pharyngei, palato-glossi, and middle constrictor muscles.†—Much controversy has taken place on the question whether this nerve is to be regarded as ministering, partly or exclusively, to the sense of Taste; and many high authorities have ranged themselves on each side. The question involves that of the function of the Lingual branch of the 5th pair; and it is partly to be decided by the anatomical relations of the two nerves. The Glosso-pharyngeal, arising from the nucleus in the floor of the Fourth Ventricle (Figs. 220, 221) near the Olivary body, and just above the vagus nucleus, is principally distributed on the mucous surface of the fauces, and on the posterior third of the dorsum of the tongue; according to Valentin, it sends a branch forwards, on either side, somewhat beneath the lateral margin, which supplies the edges and inferior surface of the tip of the tongue, and inosculates with the Lingual branch of the Fifth. A branch also accompanies the lingual artery, which is perhaps vaso-dilator in function. The experiments of Dr. Alcock, whose conclusions are borne out by Dr. J. Reid, decidedly support the conclusion, that the gustatory sensibility of the anterior part of the tongue is chiefly due to the lingual of the Fifth, being evidently impaired by division of that nerve. On the other hand, it is equally certain that the sense of taste is not destroyed by section of the Lingual nerve on each side; and it seems also well ascertained, that it is impaired by section of the Glosso-pharyngeal nerve.—The pathological evidence bearing upon this point appears somewhat contradictory. Numerous cases have been recorded,‡ in which both common and gustatory sensation were destroyed in the parts of the tongue supplied by the Fifth pair, when that nerve was paralysed; in some of these, the loss of the sense of taste appeared to extend itself to the base of the tongue, but then there was evidence that the Glosso-pharyngeal was involved in the paralysis. On the other hand, cases of paralysis of the 5th pair are related by Mr. Noble and by Vogt,§ in which common sensation was lost, whilst the sense of taste remained in the same parts; and Mr. Noble relates another case,‖ in which there was loss of taste without impairment of common sensation. The cases of Mr. Noble and Vogt would seem to indicate that the Fifth pair does not minister to the sense of Taste; but, as Dr. J. Reid has justly observed, we have no evidence that *all* the filaments of the Fifth pair sent to the tongue were affected; and there is believed to be no case on record in which the whole of the Fifth pair, or of its third branch, was found to be diseased after death, and in which during life the

* See also Vulpian, "Rev. des Cours Scient.," t. iii. p. 754.

† See Chauveau, "Journal de Physiologie;" Brown-Séquard, 1862, t. v. p. 209.

‡ See especially the cases recorded by Romberg, in Müller's "Archiv," 1838, Heft iii.; Todd and Bowman, in "Physiological Anatomy," vol. i. p. 445; and Dixon, in "Med. Chir. Trans.," vol. xxviii.

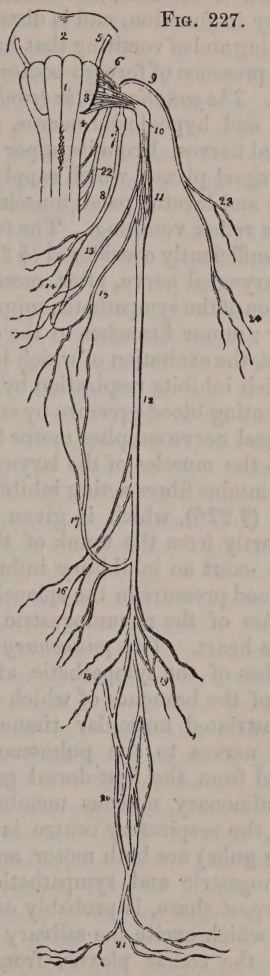
§ "Medical Gazette," Oct. 25, 1834; and Müller's "Archiv," 1840, p. 72.

‖ "Medical Gazette," Nov. 21, 1835.

sense of Taste had been retained in the anterior and middle parts of the tongue. Hence these cases only serve to indicate what is probable on other grounds—viz., that the filaments which convey gustatory impressions are not the same with those that minister to common sensation.—On the whole, then, it seems to be proved by anatomical and experimental evidence, that both the Glosso-pharyngeal and the Fifth pair minister alike to the *tactile* and to the *gustatory* sense; and there is nothing in the pathological facts just noticed, that militates against this conclusion. There seems good reason to believe the Glosso-pharyngeal to be exclusively the nerve through which the impressions made by disagreeable substances taken into the mouth are propagated to the Medulla Oblongata, so as to produce *nausea* and to excite efforts to vomit. The number of fibres in this nerve is about 3500.

451. The *Pneumogastric* nerve takes origin on each side, from a mass of grey matter in the floor of the Fourth ventricle, near the apex of the calamus scriptorius, in common with the Glossopharyngeal above and the Spinal accessory below. (Figs. 220, 221.) It emerges from the medulla oblongata between the olivary and restiform bodies by from 10 to 15 funiculi, which contain about 9000 fibres. Some of these, especially those distributed to the larynx and stomach, are motor, but the larger part of the motor nerves contained in the trunk of the pneumogastric are derived from the Spinal accessory, which gives a very large communicating branch to it shortly after its exit from the skull, and just above the ganglion of the trunk. The nerve presents two ganglia, the ganglion of the root, which is small, and includes only a few of the fibres, and a plexiform enlargement containing some ganglion cells in which the whole of the fibres are implicated. (Fig. 227.) The *ganglion of the root* is connected with the ganglion of the Glosso-pharyngeal, but the function of the connecting twig is unknown. A small meningeal branch joins with the vaso-motor branches from the sympathetic, and supplies the occipital and lateral sinuses. The presence of this nerve perhaps explains

Fig. 227.



Origin and distribution of the *Eighth Pair* of Nerves:—1, 3, 4. The Medulla Oblongata. 1. The Corpus Pyramidale of one side. 3. The Corpus Olivare. 4. The Corpus Restiforme. 2. The Pons Varolii. 5. The Facial Nerve. 6. The origin of the *Glosso-pharyngeal* nerve. 7. The ganglion of Andersch. 8. The trunk of the nerve. 9. The *Spinal Accessory* nerve. 10. The ganglion of the *Pneumogastric* nerve. 11. Its plexiform ganglion. 12. Its trunk. 13. Its pharyngeal branch forming the pharyngeal plexus (14) assisted by a branch from the glosso-pharyngeal (8) and one from the superior laryngeal nerve (15). 16. Cardiac branches. 17. Recurrent laryngeal branch. 18. Anterior pulmonary branches. 19. Posterior pulmonary branches. 20. Œsophageal plexus. 21. Gastric branches. 22. Origin of the Spinal Accessory nerve. 23. Its branches distributed to the sterno-mastoid muscle. 24. Its branches to the trapezius muscle.

the vomiting that is apt to occur in cases of strong congestion of the head, and in inflammation of the dura mater.* The *auricular* branch is given off from the ganglion of the root, and is connected with the branch from the facial. It is sensory in function, and is distributed to the auditory meatus. The attacks of coughing and of vomiting that have been occasionally reported as a consequence of the presence of foreign bodies in the meatus are attributed to irritation of this nerve. *The ganglion of the trunk* is connected with the spinal accessory, sympathetic and hypoglossal nerves, and with the loop between the first and second cervical nerves. From its upper part it sends motor and sensory branches to the pharyngeal plexus, which supply the three constrictors of the pharynx, and the tensor and levator palati muscles. Strong irritation applied to the plexus may induce reflex vomiting. The functions of the *two laryngeal nerves* have already been sufficiently considered (§ 275), but it may be here repeated that the superior laryngeal nerve, after receiving some branches from the superior cervical ganglion of the sympathetic, supplies vaso-motor branches to the superior thyroid artery; motor branches to the crico-thyroid muscle; sensory branches to the larynx, the excitation of which induces coughing; centripetal fibres, stimulation of which inhibits respiration by closure of the glottis; and lastly, pressor fibres, augmenting blood-pressure by stimulating the vaso-motor centre. The inferior laryngeal nerve supplies motor fibres to the pharynx, œsophagus, and trachea, and to the muscles of the larynx, with the exception of the crico-thyroid. It also contains fibres acting inhibitorily on the respiratory centre. The *depressor* nerve (§ 226), which is given off partly from the superior laryngeal nerve and partly from the trunk of the pneumogastric, contains centripetal fibres, which exert an inhibitory influence on the vaso-motor centres, diminishing the blood pressure in the splanchnic area, and retarding the pulse. The *cardiac branches* of the pneumogastric contain inhibitory, motor, and sensory fibres for the heart. The *pulmonary branches* of the pneumogastric are joined by branches of the sympathetic, after forming an anterior and posterior plexus, some of the branches of which contain ganglion cells, give motor branches to the unstriated muscular tissue of the trachea, bronchi, and bronchia; vaso-motor nerves to the pulmonary vessels, probably chiefly, if not altogether, derived from the first dorsal ganglion of the sympathetic; sensory fibres for the pulmonary mucous membrane throughout; centripetal fibres through which the respiratory centre is excited. The *œsophageal* fibres (forming the plexus gulæ) are both motor and sensory. The *gastric plexus*, formed by the pneumogastric and sympathetic fibres, the left pneumogastric contributing the largest share, is probably essentially motor, but contains some centripetal fibres which excite the salivary secretion. The larger part of the right vagus enters the cœliac plexus, from which fibres accompanying the arteries are distributed to the liver, spleen, pancreas, small intestine, kidneys, and adrenals. Those to the intestine and spleen are motor; those to the other viscera are partly centripetal and partly vaso-motor. Landois gives the following list of centripetal fibres as existing in the Pneumogastric:—Fibres acting on the *vaso-motor centre*, including pressor and depressor fibres; Fibres acting on the *respiratory centre*, including centripetal and inhibitory fibres; Fibres exerting an *inhibitory* action on the *heart*, probably acting in a reflex manner; Fibres acting on the centre for vomiting; Fibres acting inhibitorily on the pancreatic secretion; and, lastly, Fibres exciting reflectorially the formation of sugar in the Liver.

452. In regard to the functions of the *Spinal Accessory* nerve, also, there has been great difference of opinion; the peculiarity of its origin and course

* Landois, "Lehrbuch der Physiologie des Menschen," 1880, p. 684.

having led to the belief, that some very especial purpose is answered by it. It may be said to have three roots of origin (Lockhart Clarke)—one from the anterior grey substance of the Spinal Cord, a second from the nucleus of the Hypoglossal nerve, and a third from the tract of vesicular substance in the Medulla Oblongata, common to it and the Vagus nerve. (Fig. 220, xi.). The trunk contains from 2000 to 2500 tubules. The predominance of motor fibres in its roots, its inosculation with the Pneumogastric, and its probable reception of sensory fibres from the latter, whilst imparting to it motor filaments, have been already referred to. As its trunk passes through the foramen lacerum, it divides into two branches; of which the internal, after giving off some filaments that assist in forming the pharyngeal branch of the Vagus, becomes incorporated with the trunk of that nerve, supplying to it the inhibitory cardiac fibres which run in the Vagus; for if the roots of the spinal accessory be torn out, the inhibitory fibres undergo fatty degeneration, and after the lapse of five or six days stimulation of the Vagus is no longer followed by an inhibitory effect on the movements of the heart, whilst extirpation of the spinal accessory roots is immediately followed by acceleration of the pulse. The external division of the spinal accessory proceeds outwards, and is finally distributed to the sterno-mastoid and trapezius muscles, some of its filaments inosculating with those of the cervical plexus. It receives from the cervical nerves fibres ministering to the special muscular sense of the muscles it supplies. When the external branch is irritated, before it perforates the sterno-mastoid muscle, vigorous convulsive movements of that muscle and of the trapezius are produced; but the animal does not give any signs of pain, unless the nerve be firmly compressed between the forceps, or be included in a tight ligature. Hence it may be inferred that the functions of this nerve are chiefly motor, and that its sensory filaments are few in number. Further, when the nerve has been cut across, or firmly tied, stimulation of the lower end is attended by the same convulsive movements of the muscles: whilst stimulation of the upper end in connection with the spinal cord, after section of the Pneumogastric Nerves, is unattended with any muscular movement. Hence it is clear that the contractions in the sterno-mastoid and trapezius muscles, occasioned by irritating it, are of a direct, not of a reflex character; though the movements which occur in the laryngeal and pharyngeal muscles, on stimulation of the centric extremity, are unquestionably reflex in their nature. The functions of this nerve in regard to Respiration were examined by M. Cl. Bernard;* who has arrived at the conclusion that the Spinal Accessory is essentially a motor nerve, whose action is not exclusively requisite for the *ordinary* movements of respiration, these being provided for by the Pneumogastric and ordinary Spinal nerves; but that its special function is to bring the respiratory movements into accordance with the requirements of Animal life, adapting the actions of the muscles of the larynx and thorax to the production of *voice*, or to general muscular *effort*. The internal branch, which is specially distributed, with the fibres of the Pneumogastric, to the pharynx and larynx, is peculiarly subservient to the former of these purposes; and the external to the latter. This conclusion is sufficiently in accordance with the results obtained by other experimenters, to be received as a probable explanation of the facts which have been observed by them.

* 'Récherches Expérimentales sur les Fonctions du Nerf Spinal,' in "Archives de Médecine," 1844. See also M. Bernard's "Leçons sur la Phys. du Système Nerveux," tom. ii. p. 279 *et seq.*, 1858. M. Vulpian, "Rev. des Cours Scient.," tom. iii. p. 754; and Heidenhain, "Stud. des Physiolog. Inst. zu Breslau," 165, p. 115. Heidenhain, Schiff and Hilton think the Spinal Accessory ministers to both the ordinary respiratory and to the phonetic movements of the larynx.

453. The *Hypoglossal* nerve, or *Motor Linguæ*, the only one that now remains to be considered, contains from 4500 to 5000 nerve-fibres. Its origin is shown in Figs. 220 and 221. That the distribution of this nerve is restricted to the muscles of the tongue, is a point very easily established by anatomical research; and accordingly we find that, long before the time of Sir C. Bell, Willis had spoken of it as the nerve of the motions of articulation, whilst to the Lingual branch of the 5th pair he attributed the power of exercising the sense of taste; and he distinctly stated, that the reason of this organ being supplied with two nerves, is its double function. The inference that it is chiefly, if not entirely a *motor* nerve, which has been founded upon its anatomical distribution is supported also by the nature of its origin, which is usually from a single root, corresponding to the anterior root of the Spinal nerves. Experiment shows that when the trunk of the nerve is stretched, pinched, or galvanized, violent movements of the whole tongue, even to its tip, are occasioned; and also that similar movements take place after division of the nerve, when the cut end most distant from the brain is irritated. When this nerve is divided on one side, the tongue, on the patient being directed to put it out, is projected *towards* the palsied side: this is due to the want of action of the Lingual muscles of that side, which do not aid in pushing-forward the tip; the point is consequently directed only by the muscles of the other side, which will not act in a straight direction, when unantagonized by their fellows; on retraction it is drawn towards the sound side. It is a curious fact, however, that in paralysis from disease the Hypoglossal nerve seems not to be always palsied on the same side with the Facial, but sometimes on the opposite side, an explanation of which may perhaps be found in the disease affecting the decussating fibres described by Duval.* In regard to the degree in which this nerve possesses sensory properties, there is some difference of opinion among physiologists, founded, as it would seem, on a variation in this respect in different animals. Indications of pain are usually given when the trunk is stimulated after its exit from the cranium, and when the tongue is pinched after division of the 5th, but these proceed from its free anastomosis with the loop of the first two cervical nerves, which not improbably impart sensory fibres to it. In some Mammalia, as in the ox, cat and rabbit, the Hypoglossal nerve has been found to possess a small posterior root with a ganglion; in the last named animal, Valentin states that the two trunks pass out from the cranium through separate orifices, and that, after their exit, one may be shown to be sensory, and the other to be motor. Hence, this nerve, which is the lowest of those that originate in the cephalic prolongation of the spinal cord generally known as the Medulla Oblongata, approaches very closely in some of the higher Vertebrata to the regular type of the spinal nerves; and in the frog and some other Amphibia, it is not a cranial nerve at all, but is represented by the first pair of cervical nerves, and though in Man it still manifests an irregularity, in having in general only a single root, yet a double origin has been observed in one instance by Vulpian, whilst the irregularity is often shared by the first cervical nerve, which also has sometimes an anterior root only.†—The Hypoglossal nerve is distributed not merely to the tongue, but to

* It may be questioned, however, whether the Hypoglossal is really paralyzed on the opposite side from the Facial in such cases. An instance has been communicated to the Author by Dr. W. Budd, in which the Hypoglossal nerve was completely divided on one side; and yet the tip of the tongue, when the patient was desired to put it out, was sometimes directed *from* and sometimes *towards* the palsied side; showing that the muscles of either half are sufficient to give any required direction to the whole.

† See Vulpian's 'Essay on the Posterior or Ganglionic root of the Hypoglossal nerve in various animals,' "Journal de la Physiologie," 1862, p. 5.

the muscles of the neck which are concerned in the movements of the larynx;* and the purpose of this distribution is probably to associate them in those actions which are necessary for articulate speech. Though *all* the motions of the tongue are performed through the medium of this nerve, yet it would appear, from pathological phenomena, to have at least two distinct connections with the nervous centres; for in many cases of paralysis, the masticatory movements of the tongue are but little affected, although the power of articulation may be much injured or totally destroyed; and the converse is occasionally noticed. The Hypoglossal nerve, according to Vulpian,† contains vaso-motor fibres, the irritation of which causes the vessels supplying the submaxillary gland to contract. Its section is followed by the dilatation of these vessels.

454. The *general homology* of the Cephalic nerves, considered with reference to the ordinary Spinal, constitutes a study of much interest. It appears, from what has been already stated, that the Pneumogastric, Spinal Accessory, Glosso-pharyngeal, and Hypoglossal nerves, may be considered nearly in the light of ordinary Spinal nerves. They all take their origin exclusively in the Medulla Oblongata; and the want of correspondence in position between their roots and those of the Spinal nerves, is readily accounted for, by the alteration in the direction of the columns of the Spinal cord, which not only decussate laterally, but, as it were, antero-posteriorly (§ 456). The Hypoglossal, as just stated, not unfrequently possesses a sensory in addition to its motor root. The Glosso-pharyngeal, which is principally an afferent nerve, has a small motor root; but most of the motor fibres which answer to it are to be found in the Pneumogastric. That the Pneumogastric and Spinal Accessory together represent a Spinal nerve, may be regarded as probable from what has been already said of their relations.—Leaving these nerves out of the question, therefore, we proceed to the rest. Comparative anatomy, and the study of Embryonic development, alike show that the Spinal Cord and Medulla Oblongata constitute the most essential part of the nervous system in Vertebrata; and that the Cerebral Hemispheres are superadded, as it were, to this. At an early period of development, the Encephalon consists chiefly of four vesicles, which correspond with the ganglionic enlargements of the nervous cord of the Arthropoda, and mark four divisionsof the Cerebro-Spinal axis; and, in accordance with this view, the Osteologist is able to trace, in the bones of the cranium, elements which present an analogy to those that would form four vertebræ, in a much expanded and altered condition. The four pairs of nerves of special sensation,—Auditory, Gustatory, Optic, and Olfactory,—make their way out *through* these four cranial vertebræ respectively. At a later period of development other nerves are interposed *between* these; which, being *intervertebral*, are evidently more analogous to the Spinal nerves, both in situation and function. A separation of the primitive fibres of these takes place, however, during the progress of development, so that their distribution appears irregular. Thus the greater part of the sensory fibres are contained in the large division of the Trigeminus; whilst of the motor fibres, the anterior set chiefly pass forwards as the Oculo-motor and Patheticus; and of the posterior, some form the small division of the Trigeminus, and others unite with the first pair from the Medulla Oblongata to form the Facial. This last fact explains the close union which is found in Fishes and some Amphibia, between that nerve and those proceeding more directly from the Medulla Oblongata. According to Valentin, the Glosso-pharyngeal is the sensory portion of the first pair from the Medulla

* The muscles supplied by the Hypo-glossus are the Lingualis, Stylo-glossus, Hyo-glossus Genio-hyoid, Genio-hyglossus, Thyro-hyoid, Sterno-hyoid, Sterno-thyroid and Omo-hyoid.

† "Gaz. Hebdomadaire," 1873, No. 21.

Oblongata, of which the motor part is chiefly comprehended in the Facial nerve. Although we are accustomed to consider the Fifth pair as *par éminence* the Spinal nerve of the head, the foregoing statements, founded upon the history of development,* show that the nerves of the Orbit really belong to its motor portion; they may consequently be regarded as altogether forming the *first* of the *intervertebral* nerves of the cranium. The Facial and Glosso-pharyngeal appear to constitute the *second;* whilst the Par Vagum and Spinal Accessory, forming the *third* pair, intervene between this and the two Spinal, of which the Hypoglossal may be considered as the first.

455. *Functions of the Spinal Axis.*—In considering the functions of the Spinal Cord, we have to regard it under two aspects;—in the first place, as a *conductor* of nervous force between the Nerve-trunks and the Encephalic centres;—and in the second place, as itself *an independent centre* of nervous power. As a mere conductor of nervous force, its functions are the same as those of a Nerve-trunk:† for if it be divided, all the parts of the body which are solely supplied by nerves arising below the point of section are completely paralyzed, as far as regards sensibility and voluntary movement; no impressions made upon them having the least power to affect the consciousness, and no exertion of the will being able to determine contraction of their muscles. This state of *paraplegia*, which may be experimentally induced in animals, is frequently exhibited in Man as a result of injury or of disease which seriously implicates the Spinal Cord; and as it has been shown that among the lower animals complete reunion of the Cord may take place after complete division, as indicated by the entire restoration of its functional powers and the complete redintegration of its structure,‡ so have we reason to believe that a similar regeneration may take place to a considerable extent in Man, this being marked by the gradual return of sensibility and power of voluntary movement in the lower limbs which had been at first completely paralyzed. This regeneration is of course less likely to occur in cases of disease, when the parts around are in an unhealthy state, than when the paralysis is due to injury, which all the restorative powers of the system are engaged in repairing; but it is to be remembered, that as the injuries which are likely to cause such lesions of the Cord are nearly always attended with severe concussion (it being very rare for the Cord to be accidentally wounded by the penetration of a sharp instrument between the vertebræ, in the mode in which experiments are made upon animals), some of their first effects are attributable to the *shock* which it has sustained; so that the partial recovery which takes place at an early period must not be regarded as the result of regeneration of nervous tissue, which requires a much longer time for its completion. —The conducting power of the entire Spinal Cord being thus established, we have next to inquire whether any difference in endowment can be shown to exist in its several columns.

456. *The Spinal Cord considered as a conductor of sensory impressions and motor impulses.—The posterior columns.*—The posterior columns present two groups of fibres. A median set, known as Goll's column (*c*, Fig. 228), which consists of fibres connecting the posterior roots of the spinal nerves with the grey

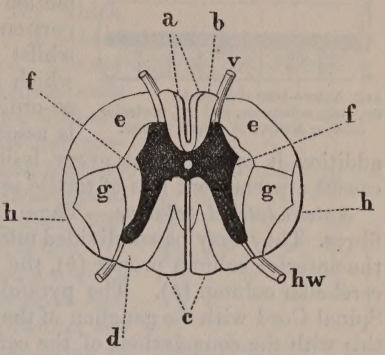
* On this point, as well as on the functions of the Cephalic nerves generally, see Prof. Valentin, "De Functionibus Nervorum Cerebralium et Nervi Sympathici," Bernæ, 1839.

† Valentin ("Die Zuckungsgesetze des lebenden Nerven und Muskels," 1863, p. 86) observes that the whole spinal cord behaves like a large nerve on applying electrical stimulation to it, though its irritability is very rapidly exhausted.

‡ See M. Brown-Séquard, in "Gazette Médicale," 1849, No. 45, and 1850, No. 30; also the "Comptes Rendus de la Société de Biologie," 1849, 1850.

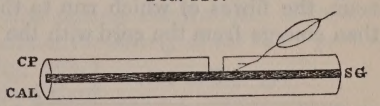
nucleus of the funiculus gracilis of the medulla oblongata, whilst the second set, constituting Burdach's cuneate column (*d*), is composed of horizontal fibres of the posterior roots passing to the grey substance, and of longitudinal fibres of the posterior roots and the grey substance ascending to the medulla oblongata. The concurrent testimony of nearly all obervers shows that the posterior columns are highly sensitive, the slightest irritation applied to their surface causing the animal (in the case of the rabbit, dog, and others) to give indications of pain; whilst, after division, stimulation of their cut surfaces not only causes pain, but in many instances induces convulsive movements. The pain is attributable, not to the fibres of the columns themselves, but to the posterior roots of the nerves which traverse them. For, if the Spinal Cord be laid bare, and a few minutes allowed to elapse to permit the immediate effects of the shock and exposure to pass off, the sensibility of the skin of the hind limbs will be found to be everywhere perfect. If a section be now made through the posterior columns (C P, Fig. 229) by passing a tenaculum from side to side and cutting down upon it, and any nerve (N) connected with a part of the cord below the section be stimulated as by pricking, the cries and movements of the animal show clearly that the conduction of painful impressions is not materially interfered with. On the other hand, if after the same preliminary proceedings, the whole of the Spinal Cord be divided transversely (CAL, SG, Fig. 230), with the exception of the posterior columns (CP), it will be found that the sensibility of the posterior limbs is entirely abolished. It is clear, therefore, that the posterior columns are not essentially formed by the continuation of the posterior roots of the spinal nerves. The circumstance that after division of these columns the surface of both the caudal and cephalic segments of the cord is acutely sensitive, is considered by M. Brown-Séquard to be due to the fact that some of the sensory fibres of the posterior roots (Fig. 239) ascend, whilst others descend a little way in these columns before crossing to the opposite side. The view which has been of late gaining ground is that they consist essentially of commissural fibres (as seen in Fig. 231 and at F, Fig. 239), which bring different segments of the cord into connection, and thus effect the co-ordination of complicated reflex movements. On this view, sensory impressions are conducted by the posterior roots to the ganglionic cells in the posterior cornua of the grey substance; from these cells commissural fibres are given off which ascend in the posterior, and perhaps also in the anterior white columns. A communication is thus established with the cells from which the motor fibres are given off that emerge with the anterior roots, and

FIG. 228.



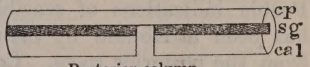
Regions and paths of conduction of the spinal cord at the level of the third Dorsal Vertebra. The grey matter is black; *v*, anterior root; *hv*, posterior root; *a* and *g*, pyramid-columns; *b*, chief fasciculus of the anterior column; *c*, Goll's column; *d*, cuneate fasciculus of Burdach; *e* and *f*, mixed lateral columns; *h*, cerebellar columns.

FIG. 229.



N, Nerve. P C, or C P, Posterior column divided. G S, or S G, Grey Substance. CAL. Antero-lateral column.

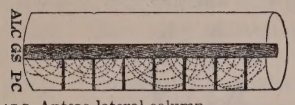
FIG. 230.



c p, Posterior column.
s g, Grey substance.
cal, Antero-lateral column.

different groups of muscles are in this way brought into combined action. In support of this view is the fact that if the posterior columns are divided at several successive planes, the movements of locomotion become more and more disordered in proportion to the number of the sections (Fig. 231), whilst it is well known that locomotor ataxy, in which affection the power of locomotion and of co-ordinating movements is remarkably impaired, is associated with disease of these columns. In addition it appears that every lesion of them in the lower part of the cord causes a permanent loss of tactile sensibility.*

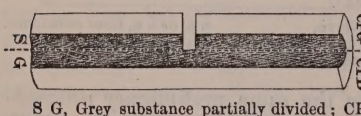
Fig. 231.



ALC, Antero-lateral column.
GS, Grey substance, and PC, posterior column divided at several points.

Antero-lateral columns.—These columns contain both motor and sensory fibres. They may be subdivided into the pyramid columns (*a* and *g*, Fig. 228), the anterior column proper (*b*), the mixed lateral columns (*e* and *f*), and the cerebellar column (*h*). The pyramid columns connect the grey matter of the Spinal Cord with the ganglion of the pes of the cerebral peduncle, and through this with the convolutions of the cerebrum. The anterior column proper and the mixed lateral columns act as commissures between the reflex centres in the grey matter of the cord and in the medulla oblongata; they contain also the fibres which, ascending in the cord, are the direct continuation of the anterior roots of the spinal nerves. They probably conduct volitional impulses to the groups of motor cells (L, Fig. 239) in the anterior cornua of the grey substance. The cerebellar columns connect the cerebellum with the grey substance of the spinal column, probably with Clarke's columns. Another important set of motor fibres running in the lateral columns is the *vaso-motor* tract, the fibres of which run to the ganglion cells of the grey substance, and then emerge from the cord with the anterior roots, after which they are either directly distributed to the vessels, or join the rami communicantes and enter the sympathetic plexus by which the vessels are surrounded. The fibres subservient to the inhibition of tactile reflex actions descend through the anterior columns of the cord.† The volitional motor fibres, though responding readily to their natural stimulus, answer but slowly to direct irritation. Feeble indications of sensibility can be obtained on irritating them, which has been attributed by Claude Bernard to the presence of recurrent fibres from the posterior roots. Convulsive movements occur in disease (Sclerosis, Charcot) of these columns. If a section of the cord be made dividing

Fig. 232.



S G, Grey substance partially divided; CPD, right posterior column; CPG, left posterior column divided.

* Schiff, "Centralblatt," 1872, p. 774. See also "Lond. Med. Record," Jan. 15, 1873. Landois, "Lehrbuch der Physiologie," 1880, p. 713. Schiff agrees with Sanders Ezn, who has found that the sensory fibres of the posterior roots in the lumbar region run obliquely upwards for two or three inches before they enter the posterior columns. The posterior colums of the lumbar region in animals (dogs) contain the sensory nerves of the organs of generation, pelvis, anus, and tail. The tactile nerves of the feet lie in other regions of the cord. Hence lesions of the posterior columns in the upper part of the lumbar segment cause anæsthesia in the region of the anus, while the sensation and motion of the posterior extremities remain normal.

† Schiff believes that in lesions of almost any part of the cord a compensatory assumption of the functions of the injured parts by those left intact may take place. The only exception being in the case of the posterior columns. He proposes the term 'Kinesodic' (κίνησις, motion, ὁδός, a path) substance for the tissue by which motor impulses are conveyed along the spinal cord, and he believes the smallest portion is capable of transmitting motor impulses in any direction.

the anterior and lateral columns, all voluntary power on the side of the section is lost. Some diminution, though not entire abolition of voluntary control over the movements of the posterior extremities of the same side is caused by division of the posterior columns and grey substance; the reason for which is clear from an examination of Fig. 233. It is here seen that section of the antero-lateral column (*a b*) divides all the fibres connecting the motor cells in the anterior horns of the grey substance with the brain; whilst section of the grey substance and posterior columns (*c d*) only destroys a certain number of the cells and their communications with the brain, those above and below remaining uninjured, and therefore retaining their activity. Section of one antero-lateral column does not produce quite complete paralysis of the parts on the same side supplied by nerves issuing from the cord behind the section, and it would seem probable that some of the motor fibres run in the anterior parts of the grey substance. In the region situated above the last three cervical vertebræ there is a strand of white substance in the lateral column which serves as the path by which the motor impressions exciting the thoracic movements in respiration are conducted. Lesions of these strands cause absolute and permanent paralysis of the respiratory movements, never compensated by any of the other parts of the cord. Section of the lateral column in the upper cervical region causes, along with a greater or less anæsthesia, complete immobility of the ribs during respiration. *The fibres which transmit motor impulses decussate almost exclusively at the lower part of the Medulla Oblongata.* (See *a r*, Fig. 234.) Hence, if a section of one-half of the Spinal Cord be made (as at 3, Fig. 234), loss of movement on the *same side* occurs, in consequence of the division of the ascending motor fibres (*a r*) from the anterior roots; whilst if the section be made at the level of the decussation of the anterior pyramids (as at 2), paralysis of the muscles of both sides is produced; lastly, if a section be made a little higher (as at 1), paralysis of the muscles of the opposite side results. The presence of various groups of *sensory* fibres in the antero-lateral columns may be regarded as established. Amongst these the most important are those which conduct sensations of *temperature, pressure,* and of *muscular sensibility*,—*i.e.*, the degree of contraction of the muscles. These appear to enter the cord with the posterior roots of the spinal nerves, and to join the ganglion cells in the posterior cornua, from which they pass into the lateral column of their own side, and ascend to the higher centres. *Afferent pressor* fibres also enter the cord with the posterior roots of the spinal nerves, and ascend in the lateral columns. These, after undergoing complete decussation, terminate in the vaso-motor centre, situated in the medulla oblongata. *Depressor* fibres must also be contained in the cord, but the precise position they occupy is unknown. Division of the anterior columns of the cord is followed by a

Fig. 233.

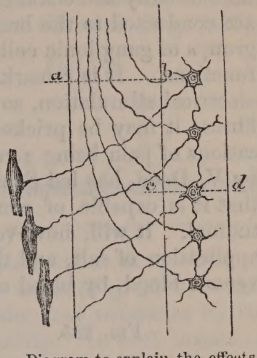


Diagram to explain the effects of division of the antero-lateral column, *a b*, and division of posterior column, *c d*.

Fig. 234.

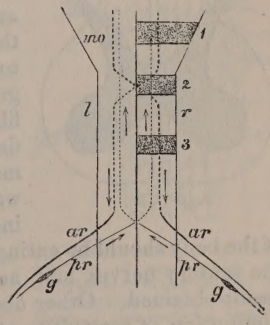
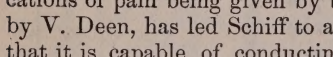


Diagram showing the course of the Motor and Sensory Fibres in the Spinal Cord and Medulla Oblongata.

remarkable tendency to spasmodic contraction in the muscles below the section.

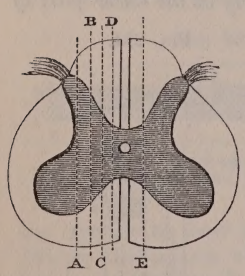
The Grey Substance of the Spinal Cord.—The grey substance of the cord is undoubtedly the channel through which most sensory and painful impressions are conducted to the brain, and in it are contained at different levels those groups of ganglionic cells or nerve centres, which preside over certain special functions. It is remarkable that it does not respond to direct mechanical or electrical stimulation, so that, notwithstanding that it contains so many sensory fibres, it may be pricked, pinched, or electrically irritated, without any indications of pain being given by the animal. This peculiarity, first pointed out by V. Deen, has led Schiff to apply the term *œsthesodic** to it, and he believes that it is capable of conducting in any direction either transverse or longitudinal. It will, however, respond to chemical stimuli, such as the direct application of salt, and the motor centres in it can be excited to action by venous blood, by blood of a higher temperature than 40° and by some poisons.

Fig. 235.



That sensory impressions are chiefly conducted through the grey substance, is shown on the one hand by retaining it intact, whilst all the white columns are divided (Fig. 235), when the sensibility of the hind limbs will be found to be but slightly impaired; and on the other hand by dividing the grey substance alone (Fig. 236), when the sensitiveness of the posterior extremities will be found to be seriously impaired. But it can be further shown by experiment, that some of the sensory fibres of the posterior roots of the spinal nerves do not ascend on their own side, but cross over to the opposite side, either immediately, or after a short ascending or descending course. Thus, if a series of sections be carried from without inwards, the first of which divides the cord as far as to the imaginary line A, Fig. 236, and the succeeding cuts be made progressively deeper and deeper as to B, C, D, and E, it will be found on testing the sensibility of the animal, that the hind limb of the side opposite to that on which the section is made, becomes progressively less and less sensitive. But if the nerve fibres ministering to common sensation on both sides decussate in the spinal cord, it must follow, that on making a longitudinal section from above downwards, along the whole length of the cord, dividing it into two lateral halves, sensibility of both sides of the body should be extinguished, for such a section would obviously divide all the sensory nerves, and, according to M. Brown-Séquard, this is actually the result obtained. Other observers,† however, though admitting there is great diminution of sensibility after a longitudinal division of the cord, maintain that distinct evidence of the conduction of sensory impressions may still be obtained. Perhaps the discrepancies in the results of the operation in the hands of different experimenters are due to different animals having been used; for M. Brown-Séquard has himself observed, that the decussation of the sensory fibres is neither so complete or immediate in Reptiles and Birds as in Mammals, and he has further noticed, that it does not seem to be so perfect in the lumbar as in the dorsal region.‡ He is of opinion that whilst the sensory

Fig. 236.



* From αἴσθησις, sensation, and ὁδός, a path. Op. cit., p. 247.

† Oré, "Comptes Rendus," t. xxxviii., 1854. Also Longet, Schiff, and Vulpian.

‡ Op. cit., p. 37.

fibres of the posterior roots in part run at once to the opposite side of the grey substance, some of them ascend and others descend for a short distance in the grey substance before decussating. Thus, if in one animal the posterior columns be divided above the origin of a particular pair of nerves, and the posterior columns be then dissected back for a short distance (Fig. 237),

Fig. 237.

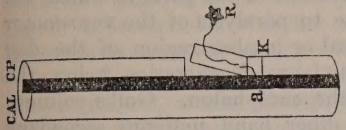
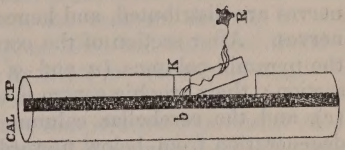
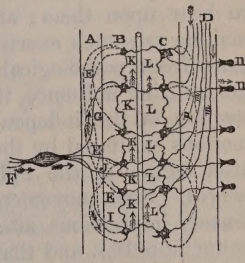


Fig. 238.



whilst in a second animal a section be made immediately below the origin of the same pair of nerves, and the same dissection be made (Fig. 238), in the former case the flap will only communicate with the grey substance by its lower extremity, and in the latter by its upper extremity. In both instances the animal will continue to give indications when the nerve (R) is pinched, that sensory impressions are still conveyed to the sensorium; thus showing that some of the fibres descend whilst others ascend in the posterior columns, for some distance before entering the grey substance, following in the two cases the course marked in the figures by the lines R, a, R, *b*. By making sections beginning at K, two centimetres from the point to which the posterior column had been reflected, where sensation was found to be still acute, and gradually approximating the attached portion of the posterior column till sensation was found to be abolished, Brown-Séquard ascertained that in the dog the posterior roots after their entry into the posterior columns spread upwards and downwards for a distance of four or five centimetres, or from an inch and a half to one inch and three-quarters before entering the grey substance. Some sensory fibres which enter motor ganglionic cells of the anterior cornua, and are subservient to reflex acts, seem to decussate nearly in the same plane as that at which they enter the cord.* Whilst it would appear that the smallest longitudinal column or transverse layer of the grey substance remaining intact, may serve to a certain limited extent as a means for the conduction of the sensory impressions of either side, it is certain that the central portions of the grey substance are the most effective in the transmission of sensations, much more so at all events than either the anterior or posterior cornua (Brown-Séquard). A very remarkable result of section of one half of the Spinal Cord is that, besides the anæsthesia which is established on the opposite side of the body, there is produced a state of exalted sensibility or *hyperæsthesia* on the same side.† This condition, made apparent by the cries of the animal on the slightest pricking or pinching of the skin, begins to appear a few hours after the operation, rapidly attains its full intensity, and

Fig. 239.



A, Posterior column. B, Posterior horn of grey matter. C, Anterior horn of grey matter. D, Antero-lateral column. E, Loop-fibres of the posterior column proper. F, A posterior nerve-root. G, Ascending fasciculus of this root. H, Direct fasciculus. I, Descending fasciculus. J, Reflex motor root. K, Chain of sensory cells. L, Chain of motor cells. *m*, Encephalic fibres of the anterior columns. N, Anterior nerve-roots. D, Loop fibres of the anterior roots.

* See Masius and Vanlair, "Centralblatt," 1870, p. 1.

† See Brown-Séquard, "Central Nervous System," 1860, p. 19.

continues to be well marked for from 17 to 22 days in dogs, and from 12 to 16 days in cats; after which, according to Schiff,* it gradually decreases, until at length the sensibility falls below its normal acuteness. M. Brown-Séquard has, however, observed it to persist in guinea-pigs, though not in a very high degree of intensity, for many months after the operation. The cause of this phenomenon has not been accurately determined. It is certainly accompanied by an increased flow of blood and increased temperature of the parts to which the nerves are distributed, and hence may be due to paralysis of the vaso-motor nerves. After section of the cord in the dorsal or lumbar region of the dog the pyramid-columns (*a* and *g*, Fig. 228) undergo degeneration below the section; their trophic centre is therefore in the encephalon. Goll's column, (*c*), and the cerebellar column (*h*), on the other hand undergo secondary degeneration from below upwards, after section of the cord, and their trophic centre is probably in the ganglia of Clarke's column (x, Fig. 228). Those fibres which do not degenerate after section are probably commissural fibres.

457. *The Cord as an independent centre.*—We have now to consider the Spinal Cord as an independent centre of nervous power, and to inquire whether the movements which are excited through its 'reflex' activity necessarily involve sensation. These movements are most characteristically displayed when the Spinal Cord is cut off from communication with the higher nervous centres; probably rather because the paths pursued by sensory impressions to the higher centres present less resistance, and are, therefore, more readily followed under ordinary circumstances (§ 459), than because (as some suppose) the impulses to reflex movements are ordinarily neutralized and rendered inoperative by an effort of the Will. It is true that those reflex actions of the Spinal Cord, which are necessary to the maintenance of Organic life, and which are equally performed whether the Spinal axis be in communication with the higher Encephalic centres or not, are continually modified or temporarily suspended by the Will; but this is only when we consciously bring the Will to bear upon them; and it is no less certain that we are *not* continually making any such exertions, in order to antagonize movements, which (as we learn from pathological evidence)† would be continually excited but for this neutralizing influence, if such a doctrine were correct.—The readiest demonstration of the independent power of the Spinal Cord is derived from the motions exhibited by the limbs of animals, when irritation is applied to them after section of the Spinal Cord at some point above the entrance of their nerves. Such movements are termed *reflex movements*, and the fact that the sensory impressions after their arrival at the Cord are reflected from it as motor impulses, and that the movements are not the product of direct stimulation applied to the part irritated, is shown by their complete cessation when the nerve trunks are divided, or the substance of the Spinal Cord is broken down. Thus, if a frog be decapitated, its body remains supported on its limbs in the usual position, and will recover this if it be disturbed; irritation of the feet will cause it to leap; and tickling the cloaca with a probe will excite

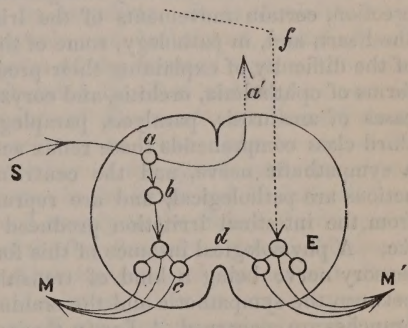
* Op. cit., p. 275.

† See, for example, the case of 'Softening of the Spinal Marrow,' recorded by Dr. Nairne in the "Med.-Chir. Trans.," vol. xxxiv.; in which a portion of the Cord at least an inch long, situated opposite the third and fourth dorsal vertebræ, was "so soft that the slightest pressure of the finger broke it up," being nearly in a fluid state through its whole thickness; yet the patient felt *pain* in his lower limbs, showing that the power of *upward* transmission remained; and although he had lost all voluntary control over the muscles of the lower part of the body, yet they were affected with incessant *choreic* movement (which, according to Dr. Hughlings Jackson, "Edin. Med. Journ.," Oct. 1868, p. 294, originates in embolism of the vessels of the Sensory Ganglia), and these movements were affected in such a marked manner by *emotions*, as plainly to indicate a *downward* transmission of motor power.

efforts to push away the instrument.* So, again, a dog in which the Spinal Cord has been divided in the dorsal region is yet capable of being excited to scratch itself with the posterior limbs, to urinate, and to perform other complex acts. It is to be observed that a slight irritation applied to the peripheral *extremities* of the afferent nerves, is a more powerful excitor of reflex action than a much stronger impression, which occasions acute pain, applied to their *trunks;* thus Mr. Grainger found that he could remove the entire hind leg of a Salamander with the scissors, without the creature moving, or any muscular contraction being produced, if the Spinal Cord had been first divided; yet that by irritation of the foot, especially by heat, in an animal similarly circumstanced, violent convulsive actions were excited in the legs and tail. This fact is important, not only as showing the comparatively powerful effect of impressions upon the cutaneous surface, but also as proving how little relation the amount of reflex action has to the intensity of sensation.

Every reflex act involves the presence of a sensory nerve, a centre composed of ganglionic cells and a motor nerve. An impression made upon the peripheric extremity of the sensory nerve is conducted towards the centre, composed of one or more ganglion cells, where it is converted into an impulse which travels along a motor or secretory nerve, and excites the muscle or gland to which it is distributed to activity. The sensory fibre is hence often called the 'centripetal' or 'afferent' nerve, whilst the other is called 'centrifugal' or 'efferent.' A stronger stimulus must be applied to a sensory nerve to induce a reflex act than is requisite to be applied directly to the motor nerve to cause the same muscle or group of muscles to contract. An example of reflex action is seen in the 'tendon reflex' of the knee, in which, if the legs are crossed and a sharp tap be given to the ligamentum patellæ, the 'quadriceps extensor' muscle instantly contracts; the rapidity and vigour of the contraction enabling important conclusions to be drawn in regard to the functional activity of the Cord. It would seem probable that the sensory or centripetal nervous fibres terminate in the ganglionic cells of the posterior horns of the grey substance of the Cord (Fig. 240). From these, processes are given off, one of which ascends on the opposite side to the sensory ganglia at the base of the Brain, whilst others terminate in cells that are in direct connection with those lying in the anterior

Fig. 240.



s. Sensory root. m. Motor root.

The ordinary course of a sensory impression to the brain is through the ganglion cell, *a*, and fibre, *a'*, which crosses to the opposite half of the cord. In the event of this being divided, the impression is transmitted through an intermediate ganglion cell, *b*, to groups of motor cells in the anterior cornua, *c*, and is thence transmitted through a motor nerve, M, to the muscles of the same side. If the impression be still stronger, the muscles of the opposite side are called into reflex action through the communicating fibre, *d*. The group of motor cells may also be called into action by the voluntary nerve, *f*, which decussates at the lower part of the Medulla Oblongata.

* It has been pointed out by Messrs. Todd and Bowman ("Physiological Anatomy," vol. i. p. 315), that the Spinal Cord of the male frog, at the season of copulation, naturally possesses a state of most extraordinary excitability. The thumb of each anterior extremity at this season becomes considerably enlarged, as is well known to Naturalists. "This enlargement is caused principally by a considerable development of the papillary structure of the skin which covers it; so that large papillæ are formed all over it. A male frog, at this season, has an irresistible propensity to cling to any object, by seizing it between his anterior extremities. It is in this way that he seizes upon, and clings to the female; fixing

horns of the grey substance. Generally speaking, sensory impressions follow the former and simplest path, and any movements that may occur are directed by and subordinate to the will; but if these ascending fibres are divided, then the purely reflex action of the Spinal Cord is exhibited, and the impression is transmitted to one cell or to a group of cells communicating with those in the anterior horn of its own side. If the impression be strong, it is transmitted to the opposite side through the connecting fibres that pass from the cells of one anterior horn, or possibly of one posterior horn, to those of the other. The motor cells of the Cord are brought into communication with the Brain, partly by fibres passing directly to the hemispheres, but chiefly through the intermediation of the cells in the Corpora Striata. The different kinds of reflex action have been well formulated by M. Küss.* They may be classified according to the direction in which both the centripetal and the centrifugal impulse passes. 1. Many of the ordinary reflex actions take place both centripetally and centrifugally through spinal nerves, examples being afforded in deglutition, coughing, sneezing, walking, and the action of the salivary glands, &c., and in pathology by vomiting, tetanus, and epilepsy. 2. A second class almost as numerous includes those reflex actions which take place centripetally through a cranio-spinal nerve, and centrifugally through a motor nerve of the sympathetic system, and most frequently a vaso-motor branch. As examples of this kind of reflex action may be given the excitation of the salivary and gastric glands, blushing or pallor of the skin, erection, certain movements of the iris, certain modifications in the beats of the heart, and, in pathology, some of those phenomena which, in consequence of the difficulty of explaining their production, are called metastatic, as certain forms of ophthalmia, orchitis, and coryza, due to reflex hyperæmia, and certain cases of amaurosis, paralysis, paraplegia, &c., due to reflex anæmia. 3. A third class comprehends those reflex actions in which the centripetal nerve is a sympathetic nerve, and the centrifugal a cranio-spinal. Most of these actions are pathological, and are represented by the convulsions that occur from the intestinal irritation produced by worms, reflex eclampsia, hysteria, &c. A physiological instance of this form occurs in respiration, the vagus or sensory nerve being a kind of transition nerve, bridging over the interval between the sympathetic and the cranio-spinal nerves, so far as its pulmonary branches are concerned. 4. Lastly, there are reflex actions in which both the centripetal and centrifugal conductors are branches of the sympathetic system. Such are the obscure actions that preside over the secretion of the intestinal juices, those which unite the various generative functions, the dilatation of the pupils owing to worms, and many pathological phenomena. From experiments on frogs and other animals, Pflüger has laid down the following "laws" of reflex action:—

his thumbs to each side of her abdomen, and remaining there for weeks, until the ova have been completely expelled. An effort of the Will alone could not keep up the grasp uninterruptedly for so long a time; yet so firm is the hold, that it can with difficulty be relaxed. Whatever is brought in the way of the thumbs, will be caught by the forcible contraction of the anterior limbs; and hence we often find frogs clinging blindly to a piece of wood, or a dead fish, or some other substance which they may chance to meet with. If the finger be placed between the anterior extremities, they will grasp it firmly; nor will they relax their grasp until they are separated by force. If the animal be decapitated whilst the finger is within the grasp of its anterior extremities, they still continue to hold on firmly. The posterior half of the body may be cut away, and yet the anterior extremities will still cling to the finger; but immediately that the segment of the Cord, from which the anterior extremities derive their nerves, has been removed, all their motion ceases. This curious instinct only exists during the period of sexual excitement; for at other periods the excitability of the anterior extremities is considerably less than that of the posterior."

* "Cours de Physiologie," 1873, p. 62.

1. *The law of unilateral reflection.*—In accordance with this law it follows that when, in consequence of irritation of one or more sensory nerves, movement takes place *on one side*, it is always on the *same* side as that to which the irritation was applied.

2. *The law of symmetry.*—It may further be demonstrated that when the impression is sufficiently strong to be irradiated to the muscles of the opposite side, these are always congenerous with those excited to action on the irritated side.

3. *The law of intensity.*—The movements on the irritated side are sometimes equalled in intensity by those of the opposite side, but if they are not equal they are always of superior vigour.

4. *Law of reflex irradiation.*—Lastly, in the *Spinal Cord*, the motor nerve excited is always on the same plane as the sensory nerve that has been irritated, but if the sensory irritation be so powerful as to be propagated beyond this point, it always affects the nerves above and never those below. In the case of the reflex movements due to the Encephalon, however, the irradiation takes place from above downwards towards the Medulla Oblongata, which possesses the power of generalizing all reflex movements; whenever the irradiated excitation in its upward course reaches the Medulla Oblongata, all the nerves arising from the Encephalon are affected.

It is noticeable also that the reflex activity is greatest in young animals. It varies in the different classes of animals, appearing to be most strongly developed in Birds, then in Mammals, and least in Fishes. It is exalted by opium, alcohol, nicotin, and especially by strychnia. It is diminished by acetate of zinc, chloral hydrate, hydrocyanic acid, belladonna, digitalis,* and bromide of potassium.† Like other parts of the nervous system the cells ministering to reflex action can be exhausted by effort and require rest to recover their properties. The experiments of Küssmaul and Tenner‡ show that interruption of the blood supply contrary to what might be expected, has a tendency to exalt the reflex excitability of the spinal cord, though to a much less extent than the nervous centres in the Brain and Medulla Oblongata; complete suppression of the blood supply to the Spinal Cord rapidly causes complete paralysis. In the case of the frog the increased excitability can be demonstrated by removing the cerebral hemispheres of the animal and allowing one of the feet to dip into a weak acid solution; after the lapse of a certain time the leg is withdrawn by a reflex act. If now the lobi optici be moistened with blood, and the experiment be repeated, a longer time is found to elapse before the movement occurs. Reflex acts are greatly enfeebled, or are altogether absent, when the blood is overcharged with oxygen, so that the reflex contractions consequent on the administration of strychnia, brucia, thebaia, and caffein are suppressed, in animals to which they have been given, by vigorous artificial respiration.§ Reflex acts are performed more rapidly than voluntary acts; more quickly by the corpora quadrigemina than by the medulla oblongata, and more quickly by the medulla oblongata than by the spinal cord. Reflex actions can also be inhibited by powerful stimulation of a sensory nerve, and also by certain poisons, as curare, digitalis, and chloroform. The time occupied in the performance of a reflex act is independent of the strength of the stimulus. The time occupied in the performance of a reflex act on the same side of the body as that on which the irritation is applied is

* Weil, "Centralblatt," 1871, p. 839. † Meihuisen, "Centralblatt," 1873, p. 88.

‡ "On the Nature and Origin of Epileptiform Convulsions," New Syd. Soc. Translation, 1859, p. 54.

§ See Leube and Uspensky, "Centralblatt," 1868, pp. 41 and 677; Uspensky, Reichert, and Du Bois-Reymond's "Archiv," 1868, p. 401.

shorter than on the opposite side, and the longer period required in the latter instance is termed the 'period of reflex conduction.' In the frog the time occupied in the performance of a reflex act on the *same* side varies from 0·008 to 0·005 sec. But to perform a reflex act on the opposite side requires a space of time longer by one-third. This difference, however, becomes very short, or almost imperceptible, when the irritation applied is very strong. Exhaustion of the spinal cord prolongs the duration of the 'reflex time.' The rapidity of conduction is not augmented by strychnia.* Cold retards it. Reflex actions may be inhibited by the will. Thus, whilst a sudden and loud sound occurring unexpectedly causes a start or contraction of the muscles generally, the body can be kept motionless by an effort of the will, if we are prepared for its occurrence. In like manner the contraction of the orbicularis palpebrarum when the conjunctiva is touched can be controlled or prevented by a determination to keep the eyes open, and the strong disposition to smile when the nose is lightly tickled can be overridden by the will. Some reflex acts, and especially those which are not performed under the influence of the will, such as the movements of the Iris and the act of delivery, cannot be suppressed by the will. The inhibition of reflex acts may also be effected by the powerful stimulation of any sensory nerve; thus the movements consequent on tickling may be prevented by biting the tongue, and this is observed even if the nerve be the one which itself excites the reflex action as in the case of rubbing the nose to prevent sneezing. Violent pain inhibits speech and locomotion as is seen in *tic*. An inhibitory centre, known as Setschenow's centre, is situated in the Frog in the lobus opticus of each side, the removal of which is followed by increased reflex excitability of all the parts below the section, and a similar centre is believed to exist in all Vertebrata.

458. That the movements executed by the limbs of the lower animals, when these are no longer connected by the Spinal Cord with the Encephalon, but remain in nervous connection with the Cord itself, do not take place through the intermediation of sensation, might be supposed to be sufficiently proved by the simple fact, that division of the Cord in Man, and hence by inference in the lower animals, reduces the parts below to a state of complete insensibility. But, on the other hand, the very performance, by decapitated animals of inferior tribes, of actions which had not been witnessed in Man under similar circumstances, has been held to indicate that the Spinal Cord in them has an endowment which *his* does not possess. The possibility of such an explanation, however unconformable to that analogy throughout organized nature, which, the more it is studied, the more invariably is found to guide to truth, could not be disproved. Whatever experiments on decapitated animals were appealed to, in support of the doctrine that the Encephalon contains the only seat of sensibility, could be met by a simple denial that the Spinal Cord is everywhere as destitute of that endowment as it appears to be in Man. The cases of profound Sleep and Apoplexy might be cited as examples of reflex action without consciousness; but these have been met by the assertion, that in such conditions, sensations are *felt*, though they are not *remembered*. It is difficult, however, to apply such an explanation to the case of anencephalous human infants (in which all the ordinary reflex actions have been exhibited, with an entire absence of brain), without supposing that the Medulla Oblongata is the seat of a sensibility which we know that the lower part of the Spinal Cord does not possess; and of this there is no evidence whatever. —Experiments on the lower animals, then, and observation of the phenomena

* See Rosenthal, Ueber Reflexe,' "Centralblatt f. d. Med. Wiss," 1877, p. 8.

manifested by apoplectic patients and anencephalous infants, *might* lead to the conclusion that the Spinal Cord does not itself possess sensibility, and that its reflex actions are independent of sensation. At this conclusion, Unzer, Prochaska, Sir G. Blane, Flourens, and other physiologists had arrived; but it was not until special attention was directed to the subject by Dr. M. Hall, that facts were obtained by which a positive statement of it could be supported. For the question might have been continually asked,—If the Spinal Cord in Man be precisely analogous in function to that of the lower Vertebrata, why are not *its* reflex phenomena manifested, when a portion of it is severed from the rest by disease or injury? The answer to this question is twofold. In the first place, simple division of the cord with a sharp instrument leaves the separated portion in a state of much more complete integrity, and therefore in a state much more fit for the performance of its peculiar functions, than it ordinarily is after disease or violent injury; and as the former method of division is one with which the Physiologist is not likely to meet in Man as a result of accident, and which he cannot experimentally put in practice, the cases in which reflex actions would be manifested are likely to be comparatively few. But secondly, a sufficient number of such instances *have* now been accumulated to prove that the occurrence is by no means so rare as might have been supposed; and that nothing is required but patient observation to throw a great light on this interesting question from the phenomena of disease. A most valuable collection of such cases, occurring within his own experience, has been published by Dr. W. Budd.*

459. So many cases of this kind have now occurred, that it may be considered as a demonstrated fact, that the Spinal Cord, or insulated portions of it, may serve in Man, no less than in the lower animals, as the centre of very energetic reflex actions, when the Encephalic power which ordinarily operates through it is suspended or destroyed, or when it is prevented from influencing the Spinal nerves by such an injury to the Cord above their points of connection with it, as prevents the transmission of nervous polarity: and it is further evident that these movements are not more dependent upon Sensation than they are upon the Will, since they may be excited without the consciousness of the individual, even when this is fully directed to the part.† And we thus have adequate ground for the assertion, that the movements which may be called forth by stimulation in the states of profound Sleep or Coma, are not to be held to indicate that conscious sensation is even momentarily excited; since we know that the reflex power of the Spinal Cord may be called into action by impressions which do not travel onwards to the sensorium, or which are powerless to affect the consciousness even when they arrive there. These abnormal reflex actions of the Spinal Cord of Man, though often powerful, have much less regularity and apparent *purposiveness*, than have the movements executed by the lower Vertebrata (as the Frog, § 457) after decapitation or section of the cord; the latter approaching, in respect to these qualities, to the reflex movements of Arthropoda—as is well seen in the following experiment, which is much relied on by those who hold that the Spinal Cord is the

* "Medico-Chirurgical Transactions," vol. xxii.

† The Author was informed by his friend Sir James Paget, that among the notes left by John Hunter (which furnished some of the materials for the admirable Catalogue of the Pathological portion of the Hunterian Museum drawn up by Sir James Paget), there was the record of a case of paraplegia, in which it appeared that Hunter had witnessed reflex movements of the legs in which sensation did not participate. When the patient was asked whether he felt the irritation by which the motions were excited, he significantly replied—glancing at his limbs,—"No, Sir; but you see *my legs* do."

seat of sensorial functions.* If a frog be decapitated and acetic acid be applied over the internal condyle of the femur, the animal will wipe away the acid with the foot of the same side; but if this be cut off, after some ineffectual efforts, and a short period of hesitation, it will perform the same action with the foot of the opposite side. The explanation seems to be that (in accordance with the laws laid down by Pflüger) when the skin of one side of the body is irritated, the motor nerves of that side respond to the impression, but this being prevented and the sensory impression continuing, the impression is radiated to the motor ganglia of the opposite side, the muscles supplied by which are accordingly brought into play. We have here exhibited the results of a mechanical disposition of parts, and not the operation of a conscious intelligence. It must not hence be inferred, however, that there is any essential difference in the endowments of the Spinal Cord, between Man and the lower animals; or that any *psychical* agency exists in the latter case which is wanting in the former. We have already seen that the existence of even the most perfectly adapted combination of different muscular actions, all obviously bearing upon a definite object, cannot in itself justify our attributing this combination to design or voluntary choice on the part of the organism that executes it (§ 404); whilst, on the other hand, to remove these movements in any case from the category of *automatic* actions, would be to assign to the Spinal Cord a power of consciously selecting and directing them, such as we have every reason for believing to be limited to the higher parts of the Cerebro-Spinal centres. Now the very *uniformity* of the movements in question, or the slight variation in effect which has been observed to follow the application of different stimuli, is itself an indication that they do *not* proceed from any purposive choice, but depend upon the special endowments of those centres of reflex action, whence the impulses that call them forth immediately issue to the nerves: and hence the more marked adaptiveness of the reflex actions performed by many of the lower tribes of animals, can only be held to indicate that a larger share of such adaptation is effected in them by what may be termed the *mechanism* of their nervous centres, and that less is left to voluntary choice and direction, which can only be safely trusted where a considerable amount of intelligence exists to guide it;—a conclusion which accords well with what has been already stated, respecting the structural differences that seem to exist between the Spinal Cord of Man, and that of the inferior Vertebrata. A peculiar condition described by Schiff† as Analgesia may here be alluded to. It consists in the retention of the capability of perceiving sensations of *touch*, though the most severe injuries to nerves produce no sensations of pain. This condition may be induced, according to Schiff, by division of the whole Spinal Cord with the exception of the posterior columns, also by rapid abstraction of blood; and it may be observed in the early stages of the administration of ether or chloroform. It seems to be questionable, however, whether this is not rather to be considered as a state of blunted common sensibility. As a sequel to the preceding consideration of the Spinal Cord as a conductor of motor and sensory impressions, and as an independent centre, the following

* See Pflüger, "Die sensorischen Functionen des Rückenmarks," Berlin, 1853; see also an able review in the "Med.-Chir. Review" for Jan. 1864, in which the above experiment is quoted. The doctrine of the independent volitional as well as sensorial power of the Spinal Cord is ingeniously sustained in Mr. G. H. Lewes's "Physiology of Common Life," vol. ii.; whilst the opposite side is taken in a review upon that work contained in the "Med.-Chir. Review," vol. xxvi. 1860, p. 423.

† "Physiologie," 1859, p. 252.

summary by M. Brown-Séquard* of the results in Man of any injury damaging the whole transverse thickness of a small portion of one lateral half of the cord is instructive. There may be observed under these circumstances:—A. On the same side—1. Paralysis of voluntary motion; 2. Hyperæsthesia for sense of contact, for tickling, for pain, and for temperature in the paralyzed parts; 3. An anæsthetic zone of small extent, corresponding to the parts supplied by nerves which take their origin from that part of the Spinal Cord situated immediately below the lesion; 4. Hyperæsthesia in a greater or less extent of surface above the zone of diminished sensibility; 5. Absolute or relative elevation of temperature in the paralyzed parts, and often also in those parts of which the sensibility is exalted, but not in the parts which are not paralyzed; 6. Phenomena indicating paralysis of the origins of the great sympathetic nerve in the neck, when the lesion has occurred in the cervico-brachial enlargement. B. On the opposite side—1. Complete anæsthesia as regards contact, tickling, pain, and temperature in the parts which correspond to those that are paralyzed on the opposite side; 2. Perfect preservation of the voluntary movements and of the muscular sense; 3. A zone of exalted sensibility of small extent and feeble in degree, situated in the parts above those the sensibility of which is diminished. From his numerous observations, he believes he is justified in drawing the conclusion already stated (§§ 456, 457), that complete decussation of the conductors of the various kinds of sensibility occurs in the cord, with the exception of those which convey the muscular sense.

460. Experiment has shown that although the grey matter of the spinal cord forms a continuous column throughout its whole length, a certain localization of function exists in it by means of which different segments are devoted to the performance of definite functions, and these may be regarded as separate centres. About eight of these centres have been distinguished—namely, 1. The centre for effecting dilatation of the pupil which is situated in the lower part of the cervical and in the upper part of the dorsal region of the spinal cord, extending as low as to the third dorsal vertebra. It is excited by the absence of light, both pupils dilating simultaneously when one eye is covered. Unilateral extirpation of this region of the cord causes the iris of the same side to contract. The motor fibres emerge in the anterior roots of the two lower cervical and two upper dorsal nerves, and enter the cervical sympathetic nerve. 2. The sweat centre (§ 377). 3. The ano-spinal centre which governs the act of defæcation and is situated in the dog at the level of the 5th lumbar vertebra. The afferent fibres of this centre are the hæmorrhoidal and the inferior mesenteric nerves; the efferent are contained in the pudendal plexus, and are distributed to the sphincter ani muscle. 4. The vesico-spinal centre. The centre for the sphincter vesicæ lies in the spinal cord of the dog at about the level of the 5th lumbar vertebra, and in the rabbit at the level of the 7th. The centre for the detrusor urinæ is, in rabbits, opposite the fourth lumbar vertebra.† 5. The centre for erection of the penis. This lies in the lumbar region of the cord. The afferent fibres are the sensory nerves of the penis; the efferent are the remarkable nervi erigentes, stimulation of which effects dilatation of the vessels of the penis, and which issue in company with the first, second, and third sacral nerves; and the branches distributed to the erector penis and transversus perinei muscles. 6. The centre for emission of semen. This, which is named Budge's "centrum genito-spinale" is also situated in rabbits

* "Journal de la Physiologie," vol. vi., Oct. 1863, published in December, 1865, pp. 124, 232, and 581; and "Archives de Physiologie," 1868, p. 610.

† Budge, "Physiologie," 1862, p. 510.

opposite the fourth lumbar vertebra. The afferent fibres are the sensory dorsal nerves of the penis. The efferent fibres emerge with the fourth and fifth lumbar nerves, and passing into the great sympathetic are distributed to the vasa deferentia and vesiculæ seminales, whilst others issue with the third and fourth sacral nerves and entering the perineal nerves, are distributed to the accelerator urinæ muscle, by which the semen is propelled from the urethra with considerable force. 7. The centre for parturition. This like the two former lies in the lumbar region, and both the afferent and efferent fibres run in the uterine plexus. 8. The vaso-motor centre. This which might more correctly be described as a series of centres governing the contraction as well as the dilatation of the vessels of certain regions or districts extends through the whole length of the spinal axis. All of these centres, in addition to the afferent fibres by which their reflex activity is ordinarily called into play, are connected with other centres in the Medulla oblongata and Brain, which are capable of exerting a powerful influence either in still further stimulating them or in arresting or inhibiting their action. When, however, the specific energy of the reflex centre is fully exerted, the superior centres cease to act upon them, and the automatic and co-ordinated character of the acts performed in subordination to them becomes manifest. This is strikingly shown in the phenomena of parturition. In this act the movements seem to be to a certain extent only dependent upon the Spinal cord; for, as will be shown hereafter (CHAP XVIII., Sect. 3), the contractions of the Uterus, which are alone sufficient to expel the fœtus when there is no considerable resistance, are not to be regarded as altogether 'reflex;' and it is only in the co-operation of those associated muscles which come into play in the second stage of labour, when the head is passing through the os uteri and is engaged in the pelvic cavity, that the assistance of the Spinal cord and its nerves is called in. These movements, like those of Defecation, may be to a certain extent promoted or restrained by voluntary effort; but when the exciting influence (the pressure of the head against the parietes of the vaginal canal) has once been fully brought into operation by the uterine contractions, the Will has little power over them, either in one way or the other. The antagonizing influence of the sphincter vaginæ seems, like that of the sphincter ani, to be dependent upon the Spinal cord; and thus it happens that when its tension and that of other muscular parts has been destroyed by death, whilst the uterus still retains its contractility, the power of the latter has sufficed for the completion of the parturient process, the child being expelled after the respiratory movements have ceased.

461. The endowments of the *Medulla Oblongata* do not seem to differ from those of the Spinal cord in any other respect than in the special nature of the reflex movements to which it ministers. This part of the Cranio-spinal axis has been regarded by some Physiologists, indeed, as the peculiar seat of vitality; since, although the other encephalic masses may be withdrawn from above, and nearly the whole of the Spinal cord may be removed from below, without the destruction of life, yet a complete stop is put to the current of vital action when the Medulla oblongata is destroyed. But the dependence of the vital activity of the body generally upon the functional integrity of this part of the nervous system, is simply consequent upon the fact that the Medulla oblongata contains the chief ganglionic centre of the Respiratory movements;* upon the integrity of which, as already shown (CHAP. IX. Sect. 3), the continuance of the Circulation is dependent, and with this, the maintenance of

* Brown-Séquard considers that the whole base of the Encephalon in Man is implicated in Respiration ("Central Nervous System," p. 191).

the organic functions generally. Where, however, as in the Frog, the respiratory activity of the skin is equal to or greater than that of the lungs, the removal of the Medulla oblongata is not attended by fatal results, and M. Brown-Séquard* has kept frogs thus mutilated, alive for eight months. Besides the respiratory, the following Ganglionic centres are situated within the Medulla oblongata:—1. The centre for effecting closure of the lids by reflex action, the afferent fibres being contained in the optic nerves and in those branches of the Fifth which are distributed to the conjunctiva and to the skin of the lids. The efferent fibres are contained in the Facial nerves, and are distributed to the orbicularis palpebrarum, corrugator supercilii, and other muscles of the face, which can exert a protective influence over the eye. This centre can be excited by an effort of the will. 2. The centre for sneezing, the afferent nerves for which are contained in the olfactory and in the Fifth pairs of nerves; whilst the efferent are contained in the spinal nerves distributed to the muscles of expiration. This centre cannot be called into action by the will. 3. The centre for coughing, the sensory fibres of which run in the vagus, whilst the motor are distributed to the expiratory muscles. 4. The centre for sucking, the afferent fibres of which run in the Fifth, and perhaps in the Glosso-pharyngeal nerves, and the motor or efferent in the branches of the Seventh pair supplying the lips. Those of the Hypoglossal to the tongue and those of the third division of the Fifth to the elevators and depressors of the lower jaw. 5. The centre for the movements of Mastication. The afferent and efferent nerves being the same as the preceding, with the addition of motor fibres from the Facial, supplying the buccinator muscle. 6. The centre for the salivary secretion, as is shown by stimulating the floor of the fourth ventricle, which causes a flow of saliva. This diminishes if the chorda tympani be divided, and ceases when the cervical sympathetic is also cut. 7. The centre for the movements of deglutition. The afferent fibres here are branches of the Fifth, Glosso-pharyngeal and Vagus nerves distributed to the mouth, gums, and pharynx, and the motor nerves are branches of the motor nerves entering into the formation of the pharyngeal plexus. 8. The centre governing the act of vomiting. 9. The centre controlling the dilatator pupillæ muscle and the smooth muscles of the orbit and lids. The fibres run partly through the Fifth and partly through the spinal cord to the cilio-spinal region, from whence they pass into the cervical sympathetic. 10. The centre of mimetic expression. 11. The centre of speech—so far as this is connected with the movements of the lips, tongue, and larynx. 12. The centres governing the movements of the heart (accelerating and inhibitory ganglia). 13. The dominant or chief part of the vaso-motor centre. 14. A centre exerting a co-ordinating influence upon the reflex centres of the spinal cord. 15. A convulsive centre, which, on being excited by the circulation through it of venous blood, or by sudden withdrawal of blood, or by mechanical lesion, liberates impulses which induce violent general convulsions. 16. The centre controlling the secretion of sweat, according to Salkowsky.

Olivary Bodies.—It is remarked by Lockhart Clarke† that it is probable the Olivary bodies are not only the centres through which different movements are co-ordinated for expressing the passions and emotions, but that they are the motor centres through which different movements are effected by sudden, violent, or peculiar impressions on the special senses; for they are intimately connected with all the sensory ganglia of the Medulla,—with the grey tubercle (trigeminus), the vagal nucleus, the post-pyramidal and restiform nuclei (auditory ganglia),

* "Central Nervous System," 1860, p. 191.

† "Philosophical Transactions," 1863, p. 319.

and the corpora quadrigemina (optic ganglia) through the fillet, and not improbably with the parts about the root of the olfactory bulb, since he has been able to trace the olivary columns nearly to the anterior perforated space. As regards the functions of the several strands composing the Medulla oblongata, little is known, excepting that the anterior pyramids are the conductors for voluntary motor impulses. The Corpora restiformia, which constitute the inferior penduncles of the Cerebellum, do not appear, according to M. Brown-Séquard,* to give passage to any of the conductors of *sensory* impressions proceeding from the trunk, limbs, or head. It is remarkable, however, that after they have been transversely divided, hyperæsthesia is produced in every part of the trunk and limbs. On the whole the Spinal cord, with its encephalic prolongation, may be said to supply by its 'reflex power' *the conditions requisite for the maintenance of the various muscular movements which are essential to the continuance of the organic processes;* and, as Dr. Hall has pointed out, it especially governs the various orifices of ingress and egress.

462. The Spinal Axis is not merely the instrument whereby the movements essential to the maintenance of the organic functions are sustained; it is also subservient to other muscular actions, whose character is essentially *protective.* Thus it was ascertained by Dr. M. Hall† that, if the functions of the Brain be suspended or destroyed without injury to the Spinal cord and its nerves, the Orbicularis muscle will contract, so as to occasion the closure of the eyelids, upon their tarsal margin being touched with a feather. This fact is interesting in several points of view. In the first place, it is a characteristic example of an adaptive action, occurring under circumstances in which volition cannot be imagined to guide it, and in which there is no valid reason to believe that sensation directs it. Further, it explains the almost irresistible nature of the tendency to winking, which is performed at short intervals by the contraction of the Orbicularis muscle; this is evidently a reflex action, capable of being in some degree restrained (like that of respiration) by the will, but only until such time as the stimulus (resulting perhaps from the collection of minute particles of dust upon the eyes, or from the dryness of their surface in consequence of evaporation), becomes too strong to be any longer resisted. The nervous channel through which this action is performed, is completed by the first branch of the Fifth and the Portio Dura of the Seventh. Again, we have in sleep or in apoplexy an example of this purely-spinal action, unbalanced by the influence of the will, which, in the waking state, antagonizes it by calling the levator palpebræ into action. As soon as the will ceases to act, the lids droop, and close over the eye so as to protect it; and if those of a sleeping person be separated by the hand, they will be found presently to return. Hence, as in studying the respiratory and other movements, we are led to perceive that it is the Brain alone which is torpid during sleep, and whose functions are affected by this torpidity. As Dr. M. Hall very justly remarks, "the Spinal system never sleeps;" it is constantly in activity; and it is thus that, in all periods and phases of Life, the movements which are essential to its continued maintenance are kept up without sensible effort.—The closure of the pupil against a strong light, is another movement of the same protective tendency. The contraction of the pupil is immediately caused by the Third pair, or Motor oculi, as is easily shown by irritating the trunk of that nerve and observing the result; but the stimulus which excites it is conveyed through the Optic nerve. Yet although the contraction of the pupil is usually in close accordance with the *sensation* occasioned by the impression of light upon

* "Philosophical Transactions," 1868, p. 27.

† "Memoirs on the Nervous System," 1837, p. 61.

the retina, yet there is evidence to prove that the sensation of light is not always necessary: for even when the sight of both eyes has been entirely destroyed by amaurosis, the normal actions have been witnessed in the pupil, in accordance with the varying degrees of light impinging on the retina. Such cases seem to indicate that the motion results from an *impression* upon the retina, which impression being conducted to the Sensorium ordinarily produces a sensation; but that even where no sensation is produced, on account of a disordered state of the part of the ganglionic centre in which the Optic nerve terminates, if the central tract which connects that nerve with the Third pair retain its integrity, the reflex contraction of the pupil may still be excited through it. The rarity of the occurrence is easily accounted-for, by the fact that in most cases of amaurosis the disease lies in the retina or in the trunk of the nerve, and thereby checks both its spinal and its encephalic actions.—Although we are not at present acquainted with any similar protective movements in the Human being, designed to keep the organ of Hearing from injury, yet there can be little doubt that those which we are constantly witnessing in other animals possessed of large external ears, are reflex actions excited by the irritation applied to them. In regard to the Nose, we find a remarkably complex action—that of Sneezing—adapted to drive-off any cause of irritation (§ 281). The stimulus is conveyed, in this case, not through the Olfactory nerve, but through the Fifth pair; so that it is not dependent upon the excitation of the sensation of Smell. The act of Coughing, also, may be regarded as of a protective character; being destined to remove sources of irritation from the air-passages. Many of the automatic movements performed by the limbs of Frogs and other animals, when their connection with the brain has been cut off, appear destined to remove these parts from sources of irritation or injury; and they may thus be rightly placed under the same category.

463. The fact that Sensation is very commonly *associated with* the reflex action we have been considering, being produced by the impression that excites them, has led many to suppose that it necessarily participates in them; a doctrine which we have seen to be untenable. But the question not unnaturally arises, *why* Sensation should so constantly participate in these operations, if not essential to them; and the answer to this question is to be found in the fact, that it is only through sensation that a higher set of actions, mental and bodily, is called into play, which is essential to the *continued maintenance* of those belonging to the present category. Illustrations of this truth might be drawn from any of the functions already noticed; but the ingestion of food will supply us with one of the most apposite. We have seen that the act of Deglutition is in itself independent of sensation; anything that comes within the grasp of the pharyngeal constrictors being conveyed downwards by their reflex contraction, just as anything which touches the arms of a Polype is entrapped by them and drawn into the stomach. But this action is attended with sensation, in the ordinary condition of the higher Animal, apparently in order that guidance may be thus afforded in the performance of those other movements of prehension, mastication, &c., by which the food may be brought within reach of the apparatus of deglutition; and the sensations which are linked with these are among the influences which prompt to those higher mental operations, whereby food is provided for the digestive apparatus to make use of. The Cœlenterate is dependent for its supplies of aliment upon what the currents in the surrounding fluid, or other chances, may bring into its neighbourhood; and if these should fail, it starves. The anencephalous Infant, again, can swallow, and even suck; but it can execute

no other movements adapted to obtain the supply of food continually necessary for its maintenance, because it has not a mind which sensations could awake into activity. The sensation connected with excito-motor actions has not only this important end, but it frequently contributes to enjoyment, as in Suction and in Emissio Seminis. The sensation accompanying the actions of this class, moreover, frequently affords premonition of danger, or gives excitement to supplementary actions destined to remove it, as in the case of Respiration; for where anything interferes with the due discharge of the function, the uneasy sensation that ensues occasions unwonted movements, which are more or less adapted to remove the impediment, in proportion as they are guided by judgment as well as by consciousness. Again, sensation often gives warning against inconvenience, as in the excretory functions; and here it is very evident, that its purpose is not only (if it be at all) to excite the associated muscles necesary for the excretion, but actually to make the Will set up the antagonizing action of the sphincters (§ 101).

464. We have now to inquire how far the independent action of the Spinal cord is concerned in the general muscular movements of Man, and especially in the locomotive actions of his inferior extremities. On this point, it is obvious that we must not be guided by the analogy of the lower animals; since the locomotive and other movements of Man are for the most part volitional and purposive, and he has to acquire by experience that control over his muscular apparatus which is necessary to enable him to perform them; whilst in Invertebrata generally, and in a large part of the lower Vertebrata, it is evident that the movements of progression, &c., which are characteristic of each species, come under the general category of automatic actions, and are provided for in the original organization of its nervous centres, being performed without any education, and under circumstances which render the notion of a purpose on the Animal's own part quite untenable. In so far as these instinctive movements require the guidance and direction of sensations, they must be referred to the 'consensual' group; but clear evidence is afforded by the continuance of many of them after the removal of the centres of sensation, that they are excito-motor in their character, and that they require no higher centre than the ganglia which correspond to the Spinal cord of Man.* There can be little doubt that the habitual movements of locomotion, and others which have become 'secondarily automatic,' may be performed by Man (under particular circumstances) through the agency of the Spinal cord alone, under the guidance and direction of the Sensorial centres, or even without such guidance; the required condition being, that the influence of the Cerebrum should be entirely withdrawn. Thus, numerous instances are on record, in which soldiers have continued to *march* in a sound sleep; and the Author has been assured by an intelligent witness, that he has seen a very accomplished pianist complete the performance of a piece of music in the same state.† A case has been mentioned to him by his friend Dr. William Budd, of a patient labouring under the form of epilepsy in which there was simply a temporary suspension of consciousness without convulsion, who, whenever the paroxysm came on, persisted in the kind of movement in which he was engaged at the moment; and thus on one occasion fell into the water through continuing to walk onwards, and frequently (being a

* See "Princ. of Comp. Phys.," §§ 649–654.

† In playing by memory on a musical instrument, the *muscular* sense often suggests the sequence of movements with more certainty than the *auditory;* and since the impressions derived from the muscles may prompt and regulate successional movements, without affecting the consciousness, there is no such improbability in the above statement as might at first sight appear.

shoemaker by trade) wounded his fingers with the awl in his hand, by a repetition of the movement by which he was endeavouring to pierce the leather. Such facts as these add great strength to the probability that when the Cerebral power is not suspended, but merely directed into another channel, as in the states of Reverie or Abstraction, and the attention is entirely drawn-off from the movements of locomotion, the continuance of these is due to the independent automatic action of the Spinal cord, the *direction* being given to them by the Sensory ganglia. This point, however, will be more fully considered hereafter; at present it may be remarked, that, when a regular train of movements is being performed under such conditions, every single action may be probably regarded as affording the stimulus to the next; each contact of the foot with the ground, in the act of walking, exciting the muscular contractions which constitute the next step;* and each movement of the musician prompting that which has customarily followed it, after the same fashion. Dr. Broadbent has called attention to an important law in reflex action, namely, that movements which are normally associated together, as for example, the contractions of the irides on exposure to light, are bilaterally co-ordinated in each centre.

465. Now in all these cases it seems reasonable to infer that the same kind of connection between the excitor and motor nerves comes to be formed by a process of gradual development, as originally exists in the nervous systems of those animals whose movements are entirely automatic; this portion of the nervous system of Man being so constituted, as to *grow-to* the mode in which it is habitually called into play. Such an idea is supported by all that we know of the formation and persistence of *habits* of nervo-muscular action. For it is a matter of universal experience that such habits are far more readily acquired during the periods of infancy, childhood, and youth, than they are after the attainment of adult age; and that, the earlier they are acquired, the more tenaciously are they retained. Now it is whilst the organism is growing most rapidly, and the greatest amount of new tissue is consequently being formed, that we should expect such new connections to be most readily established; and it is then, too, that the assimilative processes most readily take-on that new mode of action, which often becomes so completely a 'second nature,' as to keep up a certain acquired mode of nutrition through the whole subsequent life. It is an additional and most important confirmation of this view, to find that when a nerve-trunk has been cut across, the re-establishment of its conductive power which takes place after a certain interval is effected, not by the re-union of the divided fibres, but by the *development* of a new set of peripheral fibres in the place of the old ones (which undergo a gradual degeneration), this development proceeding from the point of section, and the central fibres remaining unaltered.†—That an actual continuity of nerve fibres, however, is not requisite for the establishment of those connections between excitor and motor nerves, in which the central organs take part, seems probable from the fact that under particular circumstances we find the influence of such impressions radiating in every direction, and extending to nerves which they do not ordinarily affect. Still there can be no doubt that the nerve-force is disposed to pass in special *tracks;* and it seems probable that while some of these are originally marked

* The truth of this view seems to the Author to be strongly supported by observation of the mode in which infants learn to walk; for it may often be observed that long before they can stand, they will instinctively perform the movements of walking, if they be so supported that the feet touch the ground.

† See Dr. Waller's important researches on the Reproduction of Nervous Substance, in Müller's "Archiv," 1852, Heft iv.

out for the automatic movements, others may be gradually worn-in (so to speak) by the habitual action of the Will; and that thus, when a train of sequential actions primarily directed by the Will has been once set in operation, it may continue without any further influence from that source.

466. Another manifestation of the independent power of the Spinal cord, is seen in its influence on *Muscular Tension.*—The various muscles of the body, even when there is the most complete absence of effort, maintain in the healthy state of the system a certain degree of firmness, by their antagonism with each other; and if any set of muscles be completely paralyzed, the opposing muscles will draw the part on which they act out of its position of repose; as is well seen in the distortion of the face which is characteristic of paralysis of the facial nerve on one side. This condition has been designated as the *tone* of the Muscles; but this term renders it liable to be confounded with their *tonic contraction*, which is also concerned in maintaining their firmness, but which is a manifestation of the simple contractility of their tissue, and is exhibited alike by the striated and the non-striated forms of muscular fibre, but more especially by the latter. On the other hand, the condition now alluded to, which may perhaps be appropriately termed their *tension*, is the result of a moderate though continued excitement of that contractility, through the nervous centres. It has been proved by Dr. M. Hall that the Muscular Tension is dependent, not upon the influence of the Brain, but upon that of the Spinal cord, as the following experiments demonstrate.—"Two Rabbits were taken; from one the head was removed; from the other also the head was removed, and the spinal marrow was cautiously destroyed with a sharp instrument: the limbs of the former retained a certain degree of firmness and elasticity; those of the second were perfectly lax."—Again: "The limbs and tail of a decapitated Turtle possessed a certain degree of firmness or tone, recoiled on being drawn from their position, and moved with energy on the application of a stimulus. On withdrawing the spinal marrow gently out of its canal, all these phenomena ceased. The limbs were no longer obedient to stimuli, and became perfectly flaccid, having lost all their resilience. The sphincter lost its circular form and contracted state, becoming lax, flaccid, and shapeless. The tail was flaccid, and unmoved on the application of stimuli."* It is further remarked by Messrs. Todd and Bowman, that "a decapitated frog will continue in the sitting posture through the influence of the spinal cord; but immediately this organ is removed the limbs fall apart."—This operation of the Spinal cord is doubtless but a peculiar manifestation of its ordinary reflex function. A curious experiment by M. Brown-Séquard† shows that this effect is not due to loss of contractility in the muscles; for although, after the division of the Spinal cord, there is a temporary diminution in their power, after a short interval the muscles when stimulated to contract will not only raise an equal but even a greater weight than before, the effect lasting in healthy frogs for 24 hours or more. Thus, two frogs, A and B, had weights fastened to the hind-legs until they were unable to raise them; the weighting amounted in each case to 925 grains. Immediately after divisionof the Cord they were able to raise—

	5 min. after.	15 min. after.	25 min. after.	1 hour after.	2 hours after.	4 hours after.	24 hours after.	48 hours after.
A, 308 grains.	694	925	1223	2003	2160	2160	2314	2314
B, 154 grains.	463	617	925	1540	1851	2003	2160	2160

* "Memoirs on the Nervous System," 1837, p. 93. † "Comptes Rendus," 1847.

We shall hereafter see how much the influence of the Will in producing the active contraction of a muscle is dependent upon sensations received from it; and it seems highly probable that the impression of the state of the muscle, conveyed by the afferent fibres proceeding from it to the Spinal cord, is sufficient to excite this state of moderate tension through the motor nerves arising from the latter. Such a view derives probability from the fact, which must have fallen under the observation of almost every one, that most reflex actions become increased in energy if resistance be made to them. Of this we have familiar examples in the action of the expulsor muscles which operate in defecation, urination, and parturition, if, when they are strongly excited, their efforts be opposed by spasmodic contraction of the sphincters, or by mechanical means. Many forms of convulsive movement exhibit the same tendency, their violence being proportional to the mechanical force used to restrain them. Here it is evident that the *impression of resistance* conveyed to the Spinal cord is the source of the increased energy of its motor influence; from which we may fairly infer that the moderate resistance occasioned by the natural antagonism of the muscles, is the source of their continued and moderate tension, whilst they are under the influence of the Spinal cord. This constant though gentle action serves to keep up the nutrition of the muscles which are paralysed to the will; and this is still more completely maintained, if the portion of the nervous centres with which they remain connected be so unduly irritable that the muscles are called into contraction upon the slightest excitation, and are thus continually exhibiting twitchings, startings, or more powerful convulsive movements. It is upon the continuance of the nutrition of the muscles that the persistence of their contractility depends; and hence the Spinal cord has an indirect influence upon this peculiar property, which is more likely to be retained when the muscle is still subject to the influence of the Spinal cord, though cut off from that of the Brain, than when it is completely paralysed by the entire severance of its connection with the nervous centres.

3. *Of the Sensory Ganglia and their Functions.—Consensual Movements.*

467. At the base of the Brain in Man, concealed by the Cerebral hemispheres, and connected with them through the mass of fibres known as the Corona radiata, but still readily distinguishable from them, we find the series of ganglionic masses which have been already mentioned as being in direct connection with the nerves of sensation, and which appear to have functions quite independent of those of the other components of the Encephalon. These are the olfactory and optic ganglia (Corpora quadrigemina), with the auditory and gustatory centres contained in the Medulla oblongata. The structure of the Corpora quadrigemina consists of nerve-cells, together with oblique, transverse, and longitudinal nerve-fibres resting on an arched transparent lamina, which forms the roof of the Sylvian Aqueduct.* A large portion of the optic tract is connected with the nates. The evidence obtained from anatomy, physiological experiment, and pathology, supports the view that the corpora quadrigemina, though not the centres of conscious vision, are centres of co-ordination of retinal impressions with special motor reactions.† After their removal, vision is completely abolished, and the pupils cease to act. Destruction of one optic lobe abolishes the vision of the opposite eye. In addition, destructive lesions of the Corpora quadrigemina

* Lockhart Clarke, "Proceedings of the Royal Society," June 20, 1861.

† See Ferrier, "The Functions of the Brain," 1876, p. 70.

cause disorders of equilibrium and defective co-ordination of the movements required for locomotion.* Electrical stimulation of the nates or posterior tubercle of one side causes the pupil of the opposite side, and then that of the same side, to become widely dilated. The eyeballs are directed upwards. The head is moved in the same direction as the eyeballs. There is retraction of the ears, and ultimately opisthotonos. Stimulation of the testis, or anterior tubercle, produces similar effects, with, in addition, cries. Dr. Ferrier regards them as the centres especially concerned in the reflex expression of feeling or emotion.—But besides these, at the base of the Cerebral hemispheres, we find two other large ganglionic masses on either side, through which nearly all the fibres appear to pass that connect the Hemispheres with the Medulla oblongata—namely, the *Thalami optici* and the *Corpora striata.* Now, although these are commonly regarded in the light of appendages merely to the Cerebral Hemispheres, it is evident from the large quantity of vesicular matter they contain, that they must rank as independent ganglionic centres; and this view is supported alike by the evidence of Comparative Anatomy, and by that afforded by the history of Development. For it is certain that the size of the Thalami optici and Corpora striata presents no more relation, in different tribes of animals, to that of the Cerebrum, than does that of the ganglia of Special Sense; and they may even present a considerable development, when the condition of the Cerebrum is quite rudimentary. Thus, in the Osseous fishes, a careful examination of the relations of the body, which is known as the Optic lobe makes it apparent that this is the representative, not merely of the proper Optic ganglion of Man, but also of the Thalamus opticus; whilst, again, the mass which is designated as the Cerebral lobe is chiefly homologous with the Corpus striatum of higher animals. The nature of the latter body is made apparent, in the higher Cartilaginous fishes, by the presence of a ventricle in its interior; the floor of this cavity being formed by the Corpus striatum, whilst the thin layer of nervous matter which forms its roof is the only representative of the Cerebral hemisphere. So in the Human embryo of the 6th week, we find a distinct vesicle for the Thalami optici, interposed between the vesicle of the Corpora quadrigemina and that which gives origin to the Cerebral hemispheres; whilst the Corpora striata constitute the floor of the cavity or ventricle which exists in the latter, this being as yet of comparatively small dimensions.—Now, as already pointed out (§ 445), we may distinguish in the Medulla oblongata and Crura cerebri, a *sensory* and a *motor* tract, by the endowments of the nerves which issue from them. The sensory tract may be traced upwards, until it almost entirely spreads itself through the substance of the Thalamus. Moreover, the Optic tracts and the peduncles of the Olfactory nerves may be shown to have a distinct connection with the Thalami, the former by the direct passage of a portion of their roots into these ganglia, and the latter through the medium of the Fornix. Electrical stimulation of one Corpus striatum and lenticular nucleus causes general convulsions of the muscles on the opposite side of the body without evidence of pain, whilst if these parts be destroyed, there is complete loss of voluntary power over the muscles of the opposite side of the body with preservation of the sensibility. Ferrier was unable in his experiments to detect any muscular movements on electrical stimulation of the Optic thalami. Hence we may fairly regard the *Thalami optici* as the chief focus of the *Sensory* nerves, and more especially as the ganglionic centre of the nerves of *common* sensation, which ascend

* See Serres, "Anatomie Comp. du Syst. Nerveux," 1827; McKendrick, "Trans. Roy. Soc. Edinb.," 1873; and Ferrier, loc. cit., p. 75.

to it from the Medulla oblongata and Spinal cord.—On the other hand, the *Corpora striata* are implanted on the *Motor* tract of the Crura cerebri, which descend into the Pyramidal columns; and their relation to the fibres of which that tract is composed, appears to be essentially the same as that which the Thalami bear to the sensory tract. The Corpora striata are connected with each other, on the median plane, by the *anterior* commissure; whilst the Thalami optici are united by the *soft* and the *posterior* commissures. The Corpus striatum and Thalamus opticus of the same side are very closely connected by commissural fibres, stretching from one to the other; and, if the preceding account of the respective offices of these bodies be correct, they may be regarded as having much the same relation to each other as that which exists between the posterior and anterior peaks of vesicular matter in the Spinal cord;* the latter issuing motor impulses in respondence to sensations excited through the former. They are also intimately connected with other ganglionic masses in their neighbourhood, such as the 'locus niger,' and the vesicular matter of the 'tuber annulare;' which, again, are in close relation with the vesicular matter of the Medulla oblongata.

468. It has been commonly supposed that the fibres of the Crura cerebri, after entering the Corpora striata and Thalami optici, pass continuously through these bodies, receiving 'reinforcements' of additional fibres from their ganglionic matter; and that they then radiate to the internal surface of the grey matter of the Cerebral hemispheres. Such would certainly be the conclusion to which a superficial examination of their course would lead. But very strong reasons exist for the belief that the fibres of the Crura cerebri for the most part terminate in the vesicular substance of the Corpora striata and Thalami optici; and that the radiating fibres of the Hemispheres take a fresh departure from these ganglia, serving, in fact, the part of commissures to connect *their* vesicular substance with that of the Cerebral ganglia.† And this view, as we shall hereafter see, is in complete accordance with the existence of a very decided *physiological* separation between these two sets of organs. A different view is proposed by others, according to which the motor fibres forming the corona radiata,‡ are divisible into two groups, the fibres of one of which are the channel of involuntary movements, and, after traversing the Optic thalami and Corpora quadrigemina, descend in the tegmentum of the crus cerebri without decussating till they have reached the Spinal cord, in the grey matter of which they cross and issue with the anterior roots. The other group is the channel for voluntary movements. The fibres pass from the cortex cerebri to the corpus striatum and lenticular nucleus, and, descending in the pes of the crus cerebri, form the decussation of the anterior pyramid. Still another view has lately been propounded by Flechsig,§ to the effect that the pyramids of the Medulla oblongata traverse the pons, the pes or basis of the crus cerebri, and the internal capsule without being interrupted by the presence of any ganglion cells till they reach the cortex cerebri; the fibres forming these columns would probably be the conductors of voluntary impulses.—Altogether it is very evident that a series of true ganglionic centres exist at the base of the Encephalon, which are really as distinct from either the Cerebrum or Cerebellum as the latter are from each other; and as these centres are in immediate connection with the nerves both of *special* and

* This was first pointed-out by Messrs. Todd and Bowman, in their "Physiological Anatomy," vol. i. pp. 347–350.

† See especially Messrs. Todd and Bowman's "Physiological Anatomy," vol. i. p. 277 and Prof. Kölliker's "Mikroskopische Anatomie," Band ii. § 118.

‡ Hermann, "Handbuch," vol. i. p. 304.

§ "Centralblatt f. d. Med. Wiss.," 1877, pp. 35, 614.

of *general* Sense, they may be appropriately designated the *Sensory Ganglia*. —An inquiry into the distribution and endowments of their nerves will assist us in the determination of the functions of the central organs in which they terminate.

469. *Nerves of Special Sense.*—Through the First pair, or *Olfactory* nerve, the roots of which have been traced to the cortex of the *gyrus uncinatus*, to the frontal portion of the *gyrus fornicatus*, and to the *corpus striatum*, are transmitted the impressions made by odorous emanations upon the surface it supplies; and it is not susceptible to impressions of any other kind. Anatomical examination of the distribution of this nerve proves that it is not one which directly conveys motor influence to any muscles, since all its branches are distributed to the membrane lining the nasal cavity; and experimental inquiry leads to the same result, for no irritation of the peduncles or branches excites any muscular movement. Further, no irritation of any part of this nerve excites reflex actions through other nerves. Again, it is not a nerve of 'common' sensation; for animals exhibit no signs of pain when it is subjected to any kind of irritation. Neither the division of the nerve, nor the destruction of the olfactive ganglia, seems to inconvenience them materially. They take their food, move with their accustomed agility, and exhibit the usual appetites of their kind. The 'common' sensibility of the parts contained in the olfactive organ is in no degree impaired, as is shown by the effect of irritating vapours; but the animals are destitute of the sense of smell, as is shown by the way in which these vapours affect them; for at first they appear indifferent to their presence, and then suddenly and vehemently avoid them as soon as the Schneiderian membrane becomes irritated. Moreover, if two dogs, with the eyes bandaged, one having the olfactory nerves and ganglia sound, and the other having had them destroyed, are brought into the neighbourhood of the dead body of an animal, the former will examine it by its smell; whilst the latter, even if he touches it, pays no attention to it. This experiment Valentin* states he has repeated several times, and always with the same results. Further, common observation shows that *sensibility to irritants*, such as snuff, and *acuteness of smell*, bear no constant proportion to one another; and there is ample pathological evidence, that the want of this sense is connected with some morbid condition of the olfactory nerves or ganglia.—It is well known that Magendie has maintained, that the Fifth pair in some way furnishes conditions requisite for the exercise of the power of smell; asserting that, when it is cut, the animal is deprived of this sense. But his experiments were made with irritating vapours, which excite sternutation or other violent muscular actions, not through the Olfactory nerve but through the Fifth pair; and the experiments of Valentin, just related, fully prove that the animals are not sensitive to *odours*, strictly so called, after the Olfactory nerve has been divided. The acuteness of the true sense of smell is lessened by section of the Fifth pair; but this is because the Schneiderian membrane is then no longer duly moistened by its proper secretion, and when dry it is less susceptible of the impressions made by those minute particles of odoriferous substances, to which the excitement of the sensation must be referred. A number of cases have, however, been collected by Claude Bernard, and especially a well-authenticated one (Marie Lemmens), in which, whilst no failure of the sense of smell was observed during life, the complete absence of the olfactory nerve was ascertained on post mortem examination.

470. That the Second pair, or *Optic* nerve, has an analogous character, appears alike from anatomical and experimental evidence. The roots of this

* "De Functionibus Nervorum Cerebralium," &c., Bernæ, 1839.

nerve may be traced to the *stratum zonale* and posterior part of the *optic thalamus*, to the *corpus geniculatum externum*, and perhaps also to the internum and to the *nates* or anterior pair of the corpora quadrigemina. The cortical cerebral centre is situated at the apex of the occipital lobe. No chemical or mechanical stimulus of the trunk produces *direct* muscular motion; nor does it give rise, so far as can be ascertained, to indications of pain; whence it may be concluded that this nerve is not one of 'common' sensation. That the ordinary sensibility of the eyeball remains, when the functions of the Optic nerve are completely destroyed, is well known; as is also the fact, that division of it puts an end to the power of vision. Valentin states that, although the Optic nerve may, like other nerves, be in appearance completely regenerated, he has never been able to obtain any evidence that the power of sight has been in the least degree recovered. He remarks that animals suddenly made blind exhibit great mental disturbance, and perform many unaccustomed movements; and that the complete absence of the power of vision is easily ascertained. Morbid changes are sometimes observed to take place in eyes whose Optic nerve has been divided; but these are by no means so constant or so extensive as when the Fifth pair is paralyzed; and they may not improbably be attributed to the injury occasioned by the operation itself to the parts within the orbit.

471. The Optic nerve, though analogous to the Olfactory in all the points hitherto mentioned, differs from it in one important respect—that it has the power of conveying impressions which excite *reflex* muscular motions. This is especially the case in regard to the Iris, the ordinary actions of which are regulated by the degree of light impinging on the retina. The fibres of the optic nerve that reflectorially excite the branches of the third nerve distributed to the Iris undergo partial or complete decussation in the chiasma optici.* When the Optic nerve is divided, contraction of the pupil takes place; but this does not occur if the connection of this nerve with the third pair, through the nervous centres, be in any way interrupted. After such division (if complete), the state of the pupil is not affected by variations in the degree of light impinging on the retina; except in particular cases, in which it is influenced through other channels. Thus, in a patient suffering under amaurosis of one eye, the pupil of the affected eye is often found to vary in size, in accordance with that of the other eye; but this effect is due to the action of light on the retina of the sound eye, which produces a motor change in the third pair on both sides. Further, as already shown (§ 462), the *impression* only of light upon the retina may give rise to contraction of the pupil, by reflex action, when the Optic nerve is itself sound; whilst no *sensations* are received through the eye, in consequence of disease in the sensorial portion of the nervous centres. Although the contraction of the pupil is effected by the influence of motor fibres which proceed to the sphincter of the Iris from the third pair of nerves, *through* the Ophthalmic ganglion (its dilatation, as we shall hereafter see) depends upon the influence it derives from the Sympathetic system, of which that ganglion forms part.—Besides the contraction of the pupil, another action of a 'reflex' character is produced through the Optic nerve—namely, the contraction of the Orbicularis muscle under the influence of strong light, or when a foreign body is suddenly brought near the eye. But this cannot be excited without a consciousness of the visual impression; in fact, it is a movement of a 'consensual' kind, produced by the painful sensation of light, which gives rise to the condition well characterized by the term *photophobia*.

* See Knoll, "Centralblatt," 1372, p. 265.

The involuntary character of it must be evident to every one who has been engaged in the treatment of diseases of the eyes; and the effect of it is aided by a similarly involuntary movement of the eyeball itself, which is rotated upwards and inwards, to a greater extent than the Will appears able to effect. —Another reflex movement excited through the visual sense is that of Sneezing, which is induced in many individuals by the sudden exposure of the eyes to a strong light: of the purely autonomic character of this movement there can be no question, since it cannot be imitated voluntarily; and that it is not excito-motor is proved by the fact that it is not excited unless the light be *seen.**

472. There is a further peculiarity, of a very marked kind, attending the course of the Optic nerves; this is the crossing or 'decussation' which they undergo more or less completely, whilst passing between their ganglia and the eyes. In some of the lower animals, in which the two eyes (from their lateral position) have entirely different spheres of vision, the decussation is complete; the whole of the fibres from the right optic ganglion passing into the left eye, and *vice versâ*. This is the case, for example, with most of the Osseous Fishes (as the cod, halibut, &c.); and also, in great part at least, with Birds.† In the Human subject, however, and in animals which, like him, have the axes of both eyes directed to the same object, the view entertained by many excellent anatomists and microscopists up to a recent period was that suggested by Hannover‡—namely, that the *posterior* border of the Optic Chiasma is formed exclusively of *commissural* fibres, which pass from one *optic ganglion* to the other, without entering the real optic nerve; whilst the *anterior* border of the Chiasma is composed of fibres, which seem, in like manner, to act as a commissure between the two *retinæ;* passing from one to the other, without any connection with the optic ganglia. The tract which lies between the two borders, and occupies the *middle* of the Chiasma, Hannover considers to be the true Optic Nerve; and in this he thought that a portion of the fibres decussates, whilst another portion passes directly from each Optic ganglion into the corresponding eye. The fibres proceeding from the ganglia to the retinæ, constituting the proper Optic Nerves, he distinguished into an internal and an external tract. Of these the *external*, on each side, he maintained, passes directly onwards to the eye of *that* side: whilst the *internal* crosses over to the eye of the *opposite* side. The distribution of these two sets of fibres in the retina of each eye respectively, would thus be such that, as Mayo concluded, the fibres from either optic ganglion is distributed to *its own side* of *both* eyes; the right optic ganglion being thus exclusively connected with the outer part of the retina of the right eye, and with the inner part of the retina of the left; whilst the left optic ganglion is connected exclusively with the outer side of the left retina, and with the inner side of the right. Now as either side of the eye receives the images of objects which are on the other side of its axis, it follows, if this account of the distribution of the nerves be correct, that in Man, as in the lower animals, each ganglion receives the impressions of objects situated on the *opposite* side of the body. This view is supported by the fact that extirpation of one eye in Man, as well as in Dogs and Cats (Baumgarten, Gudden), one half of both optic nerves atrophy; and it has also been shown that an antero-posterior section of the Chiasma in Cats is only followed by

* A patient was for some time in the London Hospital, in whom there was such an undue impressibility of the retina, that she could not remain in even a moderate light without a continual repetition of the act of Sneezing.

† See Solly on "The Human Brain," 2nd edit., p. 288. ‡ "Das Auge," 1852.

partial blindness. It is equally certain that varieties exist in regard to the decussation of the optic nerves in both man and animals; for other researches* seem to prove that the *decussation of the optic nerves is sometimes complete in Man*, though the fibres pursue a wavy course, which might readily lead to the assumption of the existence of the commissures and tracts above mentioned. In accordance with this is the observation of M. Brown-Séquard† that section of one optic tract causes complete amaurosis of the opposite eye, whilst an antero-posterior section of the Chiasma produces complete blindness of both eyes. A few rare cases have also been recorded in Man in which no decussation existed, so that the right optic tract became the right optic nerve, and *vice versâ*, with good vision.‡ It is possible, of course, that in such cases the decussation may have taken place in the brain. Cases have also been observed in Man in which disease of one optic tract has been accompanied by failure of vision in the corresponding upper (lower) union or outer parts of both retinæ, which necessitates a different distribution of the fibres. Where the decussation exists, its purpose may be to bring the visual impressions, which are so important in directing the movements of the body, into proper harmony with the motor apparatus; so that the decussation of the motor fibres in the pyramids being accompanied by a decussation of the optic nerves, the same effect is produced as if neither decussated—which last is the case with Invertebrate animals in general. The view maintained by Hannover receives some support from the interesting observation of Towne, that a blending of two colours occurs if their images are simultaneously presented to the *inner* side of one retina and the *outer* side of the other retina, but not otherwise.§

473. The functions of the *Auditory* nerve, or *Portio Mollis* of the Seventh, are easily determined, by anatomical examination of its distribution, and by observation of pathological phenomena, to be analogous to those of the two preceding. This nerve arises from two nuclei, the cells of which communicate. (Figs. 220, 221.) They are situated in the floor of the Fourth ventricle, at its broadest part. The anterior nucleus, which is specially connected with the Portio intermedia Wrisbergii,‖ appears to contain vaso-motor fibres. Part of the fibres arising from it runs to the cerebellum in its middle peduncle. The white striæ medullares seen on the floor of the Fourth ventricle run to the opposite pedunculus cerebelli; and some fibres, though their exact course is not known, run in the cerebral peduncle and extend to an acoustic centre in the occipital region of the cortex cerebri. Atrophy or lesion of the trunk destroys the sense of Hearing; whilst irritation of it produces auditory sensations, but does not occasion pain. From experiments made upon the nerve before it leaves the cranial cavity, it appears satisfactorily ascertained that this nerve is not endowed either with common sensibility or with the power of directly stimulating muscular movement. Nor can any obvious reflex actions be induced by stimulation of this nerve; but it seems nevertheless by no means improbable, that the muscles which regulate the tension of the Tympanum are called into action by impressions made upon it and reflected through the auditory ganglion, in the same manner as the diameter of the pupil is regulated through the optic nerve. In the involuntary start, however, which is

* Biesiadecki, "Wien. Akad. Sitz.-ber.," Band xlii., 1861, p. 86. Mandelstamm, "Centralblatt f. d. Med. Wiss., 1873, No. 22. Michel, "Archiv f. Ophthalmol.," Band xix. Heft 2, 1873.

† Brown-Séquard, "Archives de Physiologie," 1872, p. 261. ‡ Vesalius. Caldani. Lösel.

§ For additional facts bearing on this subject, see the observations of Mr. Towne 'On the Stereoscope and Stereoscopic Results,' in "Guy's Hospital Reports" for 1862, p. 69, and 1863 p. 103. ‖ Landois, "Physiologie," 1880, p. 681.

occasioned by a loud and sudden sound, we have an example of a *consensual* movement excited through the Auditory nerve, which is evidently analogous to the closure of the eyes to a strong light. In certain morbidly-impressible states of the nervous system, as will be presently shown, the effect of sounds on the motor apparatus is far more remarkable.—It has been attempted by Flourens to show that the portion of the Auditory nerve which proceeds to the Semicircular canals has functions altogether different from that portion which supplies the Vestibule and Cochlea, and that it plays an important part in the maintenance of the equilibrium of the body, a subject that will be subsequently discussed.

474. The nerves which minister to the sense of *Taste* are destitute of the peculiarities which distinguish the preceding; being no other than certain branches of ordinary afferent nerves,—the Fifth Pair and Glosso-pharyngeal (§§ 447–450)—the peculiar endowments of which seem to depend rather upon the structure and actions of the papillæ at their peripheral extremities, than upon anything special in their own character; for, as in the case of the ordinary nerves of 'common' sensation, mechanical irritation applied to them calls-forth indications of pain.—From the observations and experiments of M. Cl. Bernard and others,* it appears that the Facial nerve (portio dura of the Seventh) supplies some condition requisite for the sense of Taste, through the branch known as the Chorda tympani, which is the motor nerve of the Lingualis muscle and Sub-maxillary gland (§ 105). When paralysis of the Facial exists in Man, the sense of taste is very much impaired on the corresponding side of the tongue, provided that the cause of the paralysis be seated above the origin of the Chorda tympani from its trunk. Similar results have been obtained from experiments upon other animals. The effect may possibly be attributable to an interference with the secretion of saliva.

475. *Nerves of Common Sensation.*—To the sense of *Touch* all the afferent nerves of the body (save the nerves of special sense) appear to minister; in virtue—according to the doctrine already propounded—of the direct connection of certain of their fibrils with the *Sensorium Commune.* But the degree in which they are capable of producing Sensations does not bear any constant relation to their power of exciting reflex actions. Thus, the Glosso-pharyngeal is not nearly so *sensitive* as the Fifth pair; though more powerful as an *excitor* nerve. The Vagus appears to have even less power of arousing sensory changes; although it is the most important of all the excitors to reflex action. So, again, the afferent nerves of the inferior extremities, in Man, are less concerned in ministering to sensations, than are those of the superior; and yet they appear to be much more efficient as excitors to muscular movement.—These differences may be accounted for, by supposing that the proportion which the fibres having their centre in the ganglionic matter of the Spinal Cord, bears to that of the fibres which pass on to the Sensorium, is not constant, but is liable to variation in different nerves; the former predominating in the Vagus and the Glosso-pharyngeal, whilst the latter are more numerous in the Fifth Pair, and in most of the Spinal nerves.

476. *Motor Nerves.*—No motor nerves issue from the Sensory Ganglia with the same directness that afferent nerves proceed towards them; but the reflex actions of these centres find a ready channel in the motor nerves of the Cranio-Spinal axis generally. For, as we have seen (§ 445), the motor tract of the Crura cerebri, which is in connection with the motor Encephalic nerves, and

* "Archives Générales de Médecine," 1844. See also Lussana, Neumann, Roux, Juzani, and Baragiola.

also (through the vesicular substance of the Spinal cord) with the anterior roots of the Spinal nerves, passes up into the Corpora striata and Corpora quadrigemina. Although the direct connection of the other ganglia of Special Sense with the Motor columns is at present a matter of presumption only, yet this presumption is strongly supported by the analogy of the Optic ganglia; the distinctness of this connection in *their* case being easily accounted for, when it is remembered in how great a degree the general movements of the body are guided by the visual sense.

477. *Functions of the Sensory Ganglia.*—We have now to consider what deductions may be drawn with regard to the functions of the Sensory ganglia in Man, from the facts supplied by Comparative Anatomy, by Experimental inquiry, and by Pathological phenomena. The determination of these functions may seem to be the more difficult, as it is impossible to make any satisfactory experiments upon the ganglionic centres in question, by isolating them completely from the Cerebral hemispheres above, and from the Medulla oblongata and Spinal cord below. But the evidence derived from Comparative Anatomy appears to be in this case particularly clear; and, rightly considered, affords us nearly all the information we require. In the series of "experiments prepared for us by Nature," which is presented to us in the descending scale of animal life, we witness the effects of the gradual change in the relative development of the Sensory ganglia and Cerebral hemispheres, which are presented to us in descending through the Vertebrate scale; and the results of the entire withdrawal of the latter, and of the sole operation of the former, which are exhibited in the higher Invertebrata (see §§ 447, 450),* and we are thus led by the very cogent evidence which Comparative Anatomy supplies, to regard this series of Ganglionic centres as constituting the real *Sensorium;* each ganglion having the power of rendering the Mind conscious of the impressions derived from the organ with which it is connected. If this position be denied, we must either refuse the attribute of consciousness to such animals as possess no other Encephalic centres than these; or we must believe that the *addition* of the Cerebral hemispheres, in the Vertebrate series, *alters* the endowments of the Sensory ganglia—an idea which is contrary to all analogy.

478. So far as the results of Experiments can be relied on, they afford a corroboration of this view. The degree in which animals high in the scale of organization can perform the functions of life, without any other centres of action than the Ganglia of Special Sense, the Medulla oblongata, and the Cerebellum, appears extraordinary to those who are accustomed to regard the Cerebral hemispheres as the centre of all energy. Not only Reptiles, but Birds and Mammals, may survive for many weeks or even months (if their physical wants be duly supplied) after the removal of the entire Cerebrum.† It is difficult to substantiate the existence in them of actual *sensation;* but

* It is worthy of special notice, that the development of the Cephalic ganglia in the Invertebrata always bears an exact proportion to the development of the *eyes;* the other organs of special sense being comparatively undeveloped; whilst these, in all the higher classes at least, are instruments of great perfection, and are evidently connected most intimately with the direction of the movements of the animals. Of this fact we have a remarkable illustration in the history of the metamorphosis of Insects; the eyes being almost rudimentary, and the Cephalic ganglia comparatively small, in most Larvæ; whilst both these organs attain a high development in the Imago, to whose actions the faculty of sight is essential.

† Flourens, "Récherches Expérimentales sur les Propriétés et les Fonctions du Système Nerveux," 2nd edit., 1845. Hertwig, "Exper. de effect. læsion. in partibus Encephali," Berol., 1826. Magendie, "Leçons sur les Fonctions du Système Nerveux," Paris, 1839. Longet, "Traité de Physiologie," tom ii. partie 2, 1860, p. 411.

some of their movements appear to be of a higher kind than those resulting from mere excito-motor action. So long as the animal is kept at perfect rest, and not excited by any stimulus, tactile or otherwise, so long does it remain quiet and immovable. It is only when stimulated that it begins to move. One of the most remarkable phenomena exhibited by such a being, is the power of maintaining its equilibrium, which can scarcely exist without consciousness.* If it be laid upon the back, it rises again: if pushed, it walks. If a Bird thus mutilated be thrown into the air, it flies; if a Frog be touched, it leaps; if thrown into the water it swims. It swallows food and liquid, when they are placed in its mouth; and the digestive operations, the acts of excretion, &c., take place as usual. If the back or interscapular region be touched it croaks.† Frogs without Cerebrum, Optic thalami or Optic lobes no longer croak on stroking the back, and lose the power of maintaining their equilibrium when the board on which they are placed is slowly inclined. In the case of a Pigeon experimented on by Malacorps, which is recorded by Magendie, there appears sufficient proof of the persistence of a certain amount of sensation. Although the animal was not affected by a strong light suddenly made to fall upon its eyes, it was accustomed, when confined in a darkened or partially-illuminated room, to seek out the light parts; and *it avoided objects that lay in its way.* In the same manner, it did not seem to be affected by sudden noises; but at night, when it slept with its eyes closed and its head under its wing, it would raise its head in a remarkable manner, and open its eyes, on the slightest noise; speedily relapsing into a state of complete unconsciousness. Its principal occupation was to preen its feathers and scratch itself. And Longet mentions that a Pigeon from which he had removed the entire Cerebrum, gave many indications of consciousness of light; for not only did the pupil contract, but the lids closed, when a strong light was suddenly made to fall upon the eye, the animal having been previously kept in darkness; and *when a lighted candle was made to move in a circle before it, the animal executed a corresponding movement with its head.*‡—The condition of such beings seems to resemble that of a Man, who is in a slumber sufficiently deep to lose all distinct *perception* of external objects, but who is yet conscious of *sensations*, as appears from the movements occasioned by lights or by sounds, or from those which he executes to withdraw the body from an uneasy position.

479. The results of other experiments made upon the Sensory ganglia themselves, and upon the organs from which they derive their impressions, confirm this view; by showing that the ordinary movements are seriously perturbed, and that in some instances a new set of automatic movements is induced, when the normal relations between the sensory and motor apparatus are disarranged. Of the functions of the ganglia of special sense, those of the *Corpora Quadrigemina* are the chief which have been examined experimentally. These ganglia are connected with the *motor* columns of the spinal cord on each side by a strand of fibres thrust aside by the decussation

* Eckhard "Handbuch der Physiologie," Band i. 1879, p. 117.

† Paton, "Edinb. Med. and Surg. Journ.," vol. lxv. p. 251, April, 1846. Goltz, "Beiträge zur Lehre v. d. Functionen der Nervencentra," Pamphlet, 1869.

‡ It must not be forgotten that, in such experiments, the severity of the operation will of itself occasion a suspension or disturbance of the functions of parts that remain; so that the *loss* of a power must not be at once inferred from the absence of its manifestations. But the *persistence* of a power, after the removal of a particular organ, is a clear proof that it cannot be the peculiar attribute of that organ. See Voit's experiments on Pigeons, which, after removal of the hemispheres, recovered sufficiently to perform all their ordinary acts except that of feeding themselves. "Sitzungsber. der Bair Acad. Math. Phys. Cl." 1868.

of the pyramids, which, passing upwards and embracing the olivary body, ascends through the pons, and enters the lateral and posterior part of the testes. The decussation of some of the fibres of these strands forms the roof of the aqueduct of Sylvius. They are connected with the sensory *columns* of the cord through the tegmentum and the Optic thalami. It is probable that fibres of both optic tracts arise* from them. The experiments of Flourens and Hertwig have shown that the connection of these bodies with the visual function, which might be inferred from their anatomical relations, is substantiated. The partial loss of the ganglion on one side produces partial loss of power and temporary blindness on the opposite side of the body, without necessarily destroying the mobility of the pupil; but the removal of the larger portion, or complete extirpation of it, occasions permanent blindness and immobility of the pupil, with temporary defect of the power of co-ordinating muscular movements on the opposite side. This temporary disorder of the muscular system sometimes manifests itself in a tendency to rotation, as if the animal were giddy; but no disturbance of consciousness appears to be produced; and Hertwig states that he never witnessed the convulsions, which Flourens mentions as a consequence of the operation, and which were probably occasioned by his incision having been carried too deeply. As Longet has justly remarked, it is difficult, if not impossible, to remove one or both of these ganglionic masses, without doing such an injury to the Crura cerebri on which they repose, as shall in great degree account for such disturbed movements (§ 483). Irritation of *one* of the Corpora quadrigemina has been observed, both by Flourens and Longet, to produce contraction of the pupils of *both* eyes. Budge has corroborated Flourens' statements, adding that it is only when the lesion affects the inner part of the Corpora quadrigemina, that paralysis of the Iris occurs, and that this paralysis is on the side opposite to the lesion. Renzi admits there is temporary, but denies that there is any permanent, loss of contractility of the Iris. Knoll† found that irritation of one of the Nates caused dilatation of both pupils, but especially of that of the same side, and that lesions of the corpora quadrigemina were without effect on the iris, as long as the optic tracts were untouched; but when these were damaged between the corpora quadrigemina and the chiasma, blindness with paralysis of the opposite iris occurred. Lesions of the optic nerve on the distal side of the chiasma caused paralysis of the Iris of the same side, showing that the fibres of the optic nerve which excite reflectorially the iridal branches of the third nerve, undergo complete decussation in the chiasma. Irritation of the right anterior Corpus, first causes both eyes and then the head to turn to the left, and *vice versâ*. Ferrier found that in rabbits a slight puncture caused the animal to start suddenly and bound away as if alarmed. Electrical stimulation caused retraction of the ears, elevation of the tail, extension of the jaws, clenching of the teeth, and on increasing the strength of the stimulus, opisthotonos. Brunton noticed in Birds increase of the blood pressure, prolongation of the cardiac beats, and deeper respiration. Knoll, operating on Rabbits, did not observe any alteration in their motility after injuries inflicted upon these bodies, but other observers‡ have shown that the optic lobes in Frogs and in Birds, and the corpora quadrigemina in Mammals, exert a powerful influence in effecting the harmony and co-ordination of muscular movements and in maintaining the equilibrium of the body. The results of experiments are partly confirmed by Pathological phenomena in Man; for there are many

* See Ferrier, "Functions of the Brain," 1876, p. 70; also McKendrick, "Transact. Roy. Soc. Edinb.," 1873.

† "Centralblatt f. d. Med. Wiss.," 1872, p. 265.

‡ Cayrade, "Journ. de l'Anat.," 1868; McKendrick, loc. cit.; Ferrier, loc. cit.

instances on record in which blindness has been one of the consequences of disease in one or both tubercles; and in some of the cases in which the lesion extended to parts seated beneath the tubercles, disturbed movements were observed.—The subservience of these bodies to the exercise of the visual sense, appears, on the whole, to be the point best established in regard to their functions; and considering the degree in which this sense is concerned in the regulation of the general movements of the body, it is not surprising that lesions of its centre should occasion a perversion of these movements. This appears the more probable from the fact, that in animals whose Sensory ganglia bear so large a proportion to the whole Encephalon, that we must look upon them as the principal centres of motor activity, instead of being chiefly concerned (as in Man) in the mere guidance of movements whose origin is Cerebral, lesions of the organ of sense from which the impressions that excite the sensori-motor impulses are derived, produce a corresponding disturbance. Thus Flourens found that a vertiginous movement may be induced in Pigeons by simply blinding one eye; and Longet produced the same effect by evacuating the humours of the eye.

480. It is probably on the same principle that we are to account for the remarkable results obtained by Flourens* from section of the portion of the Auditory nerve proceeding to the semicircular canals. Section of the horizontal semicircular canal in Pigeons, on both sides, induces a rapid jerking horizontal movement of the head, from side to side; and a tendency to turn to one side which manifests itself whenever the animal attempts to walk forwards. Section of a vertical canal, whether the superior or inferior, of both sides, is followed by a violent vertical movement of the head. And section of the horizontal and vertical canals, at the same time, causes horizontal and vertical movements. Section of either canal on one side only, is followed by the same effect as when the canal is divided on both sides; but this is inferior in intensity. The movements continue to be performed during several months, but cease immediately if the Thalami optici be removed (Löwenberg). In Rabbits, section of the horizontal canal is followed by the same movements as are exhibited by Pigeons; and they are even more constant though less violent. Section of the anterior vertical canal causes the animal to make continued forward 'somersets;' while section of the posterior vertical canal occasions continued backward 'somersets.' The movements cease when the animal is in repose; and they recommence when it begins to move, increasing in violence as its motion is more rapid.—These curious results are supposed by M. Flourens to indicate that the nerve supplying the semicircular canals does not minister to the sense of hearing, but to the direction of the movements of the animal; whilst M. Cyon† refers them to the circumstance that in order that an animal should preserve its equilibrium, it should have a correct idea of the position of its own head, and that the semicircular canals supply this information in consequence of each canal having a definite relation to space. But they may also be explained upon the supposition, that the normal functions of the semicircular canals is to indicate to the animal the *direction* of sounds, and that its movements are partly determined by these; so that a destruction of one or other of them will produce an irregularity of movement (resulting, as it would seem, from a sort of giddiness on the part of the animal), just as when one of the eyes of the bird is covered or destroyed, as in the experiments previously cited. Goltz‡ has recently maintained that

* Op. cit. See also Böttcher, "Centralblatt f. d. Med. Wiss.," 1873, p. 72; and Löwenberg, idem, p. 278; Waldeyer, idem, 1872, p. 385.

† Pflüger's "Archiv," Band viii. p. 325. ‡ Ibid., Band iii. 1870, p. 172.

the position of the head is judged of by the animal from the pressure exerted by the endo-lymph on one side or the other of the semicircular canals; and that when the endo-lymph has escaped by section of the canals, neither the eye nor the muscular sense can supply the deficiency—the movements of the body are on this view secondary, and are due to the inability of the animal to judge of its relation to surrounding objects from the position of its head; on the other hand, a definite perception of the position of the head may be necessary to the maintenance of equilibrium; and this perception has its origin in the semicircular canals, each canal having a certain determinate relation to certain positions.* The derangement of motion consequent upon division of the semicircular canals, Cyon classifies under three heads:—1. Derangements of equilibrium, as a direct result of the injury. 2. Violent movements, resulting from the irritation consequent on the abnormal sense of hearing induced thereby. 3. Consecutive symptoms, occurring some days after the operation, from the resulting inflammation of the cerebellum.

481. The numerous experiments which have been made for the purpose of determining the functions of the Thalami optici and Corpora striata, have not yielded any very satisfactory results; chiefly on account of the impossibility of completely isolating them in such a manner as to limit the operation (whether this be section, removal, or irritation) to them alone. Thus it is impossible to remove them, either separately, or conjointly, without first removing the Cerebral hemispheres; and the Thalami cannot be entirely removed without dividing the stratum of fibres which traverse their deeper portion in their passage to the Corpora striata. The relations of the Thalami optici to the *visual sense* are not certainly known; for (according to the affirmation of Longet) they may be completely destroyed in Mammals and Birds, without destruction of sight or loss of the activity of the iris; whilst irritation of one or both of them produces no contraction of the iris. Renzi,† however, found that removal of the posterior part of the Optic thalamus of one side was followed by blindness and permanent dilatation of the pupil of the opposite eye, whilst Lussana and others have observed blindness of the opposite eye in cases of injury of the Thalamus in which the optic tracts and the adjoining region of the Thalamus had not been damaged. Hughlings Jackson has recorded a case in which lesion of the posterior part of the Optic thalamus was associated during life with left-sided hemiopia of both eyes. The loss of sight with dilatation and immobility of the pupil, which is frequently observed in cases of apoplectic effusions into the substance of the Thalami, may no doubt be sometimes due to the compression of the Optic nerves which lie beneath them; but there seems good reason to believe that the Thalami really constitute centres for visual impressions, since animals still clearly retain a certain amount of vision after the removal of the whole of both hemispheres. Evidence also exists to show that they have some relation to the other special senses; for although these are to some extent retained after the removal of the Optic thalami, yet there are many pathological cases showing impairment of the tactile and auditory senses with lesion of their substance. These bodies appear to possess a very decided influence on the power of *voluntary movement;* for although an animal maintains its balance, and can be made to move onwards, after the removal of the Cerebral hemispheres, and even after the removal of the Corpora striata, yet if either of the Thalami optici be removed, the sensibility and power of voluntary movement are destroyed on the *opposite* side of the body, and the animal

* See also Abstract, Knapp's "Archives of Ophth. and Otol.," 1874, p. 137.

† "Annali Universale," vol. clxxxix. p. 419.

consequently falls over to that side (Longet). If incisions equal in depth and direction be made simultaneously into certain parts of the Optic thalamus of each side in frogs from which the brain has been removed, an uncontrollable impulse to move forwards is observed; but if the incisions be not symmetrical the animal keeps turning to one side in a circular manner (*évolution du manége*): according to Longet and Lafargue, this movement is directed in the rabbit towards the opposite side; whilst Flourens states that in the frog its direction is towards the injured side; and according to Schiff* the destruction of the three anterior fourths of this organ in the rabbit determines this movement towards the injured side, whilst that of the posterior fourth determines the movement towards the opposite side. Brown-Séquard attributes the rolling movements in many of these cases to certain muscles being in a state of spasm, in other instances to vertigo. Both Schiff and Lancerotte† regard the Optic thalamus as containing a centre for the fore limb. Nothnagel‡ entirely destroyed both Thalami in rabbits without removal of the Cerebrum, and declares that they only differed from uninjured animals in not withdrawing the forepaws when these were stretched out horizontally in front of them, or if one Thalamus only was destroyed, in retaining the opposite leg in this position. No mechanical irritation of the Thalami produces either signs of pain or muscular movement; and this fact might at first appear to negative the doctrine that these organs are the ganglia of common sensation.§ But it must be borne in mind that the production of pain by mechanical injuries is by no means a universal phenomenon in the case of the nerve-*trunks* which minister to sensation—the olfactory, optic, and auditory nerves being exempted; and it need occasion still less surprise, therefore, that a nervous *centre* should be destitute of this kind of impressibility, which we have seen to be wanting also in the Spinal cord.

482. The effects of lesions of the Corpora striata are less distinctly marked. These bodies contain two masses of grey matter, a *nucleus caudatus* or intra-ventricular nucleus, and a *nucleus lenticularis*, or extra-ventricular nucleus.‖ (See Fig. 244). It is supposed by some, but it is purely hypothetical, that the corpora striata are the automatic centres of locomotion. The spring of their action lies in the functional activity of the cerebral hemispheres—that is, in the will; but when once started they may continue to act automatically, the exertion of the will being no longer required for the continuance of their movements, though it is, of course, always ready to hasten, arrest, or modify them. Nothnagel¶ found that puncture of a certain point of the nucleus caudatus of the corpus striatum, or its destruction by the injection of a minute portion of strong chromic acid caused rabbits, after a short interval, to leap and run forwards till they fell from exhaustion, and he applied the name 'nodus cursorius' to this spot. Destruction of the adjoining parts of the nucleus caudatus by the same means caused peculiar disturbance of the

* Roser and Wunderlich's "Archiv für Physiol. Heilkunde," 1846, § 667.

† "Memoire sur les Contrecoups, Prix de l'Acad. de Chir." t. iv. p. 310.

‡ Nothnagel, "Virchow's Archiv," Band lxii. p. 203.

§ Nothnagel ("Centralblatt," 1874, p. 577) states that from numerous experiments on Rabbits he has satisfied himself—1. That the optic thalami have nothing to do with the innervation of voluntary movements. 2. That after their extirpation, no disturbance of cutaneous sensibility can be demonstrated. 3. That they appear to have a definite relation to the muscular sense.

‖ Ferrier ("West Riding Lunatic Asylum Rep.," vol. iii. p. 95) found that electrical stimulation applied to one corpus striatum caused pleurosthotonos, the flexors preponderating over the extensors, but this has not been corroborated by Glikz (Eckhard's "Beiträge," Band vii. p. 177) whose investigations were superintended by Eckhard.

¶ Virchow's "Archiv," Band lvii. pp. 184, 209.

movements of the legs.* Carville and Duret observed temporary paralysis of the muscles of the opposite side after extirpation of one nucleus caudatus. Mechanical stimulation of the *Lenticular nucleus*, acording to Nothnagel, causes deviation of the legs outwards and pleurosthotonos. In lesions limited to the caudate and lenticular nuclei the muscles of the opposite side are paralyzed, probably by compression of the fibres forming the internal capsule; but this paralysis is only temporary, and when the blood is absorbed, recovery takes place. When the lesion affects the posterior part of the lenticular nucleus, the sensory fibres of the internal capsule may undergo compression, and then, in addition to the motor paralysis, there is hemi-anæsthesia of the opposite side. It was affirmed by Magendie† that there exists in them a motor power which excites *backward* movement, and that a corresponding power of exciting *forward* movement exists in the Cerebellum; that these two powers ordinarily balance one another; but that, if either organ be removed, the power of the other will occasion a continual automatic movement, the removal of the Corpora striata causing an irresistible tendency to forward progression, whilst the division of the peduncles of the Cerebellum (according to him) occasions the reverse movement. These assertions, however, have not been confirmed by other experimenters. The results of removal of the Corpora striata with the anterior part of the Cerebral hemispheres are for the most part negative;‡ for the animal usually remains in a state of profound stupor, although still retaining the erect position; and it is only when irritated by pinching or pricking that it will execute any rapid movements. Burdon-Sanderson§ has shown that by direct irritation of the Corpus striatum, movements of the muscles of the opposite side can be produced, and that there is a certain correspondence in the groups of muscles that can thus be called into play, and those that are excited by irritation of definite regions of the intact cerebral hemispheres: on irritating the deepest part of the Corpus striatum, the animal opened its mouth, and alternately thrust out and retracted the tongue.‖

483. The fibrous tracts which connect these ganglionic masses with the Medulla oblongata are designated the *Crura cerebri*. These contain four sets of fibres, of which some connect the Spinal cord with the Encephalic centres; others, springing from the grey substance of the Medulla oblongata and Pons, run towards the hemispheres; a third set arise from the grey matter of the cerebral peduncles and run forwards to the cerebrum and backwards to the cerebellum; and others again extend from the corpora quadrigemina to the cerebrum. These several fasciculi are arranged so as to form an anterior layer named the *basis*, or *crusta*, of the cerebral peduncle, which is chiefly composed of motor fibres, though the outermost strand, sometimes called the fasciculus of Meynert, is sensory; and a superior or posterior layer, named the *tegmentum*, which is composed of sensory or afferent fibres. Between the two layers are darkly pigmented ganglion cells, constituting the *locus niger*. The sensory fibres of the tegmentum enclose the *red nucleus*, which is connected both with the cerebellum and the corpora quadrigemina. If the Crura cerebri are completely divided, the result, as might be anticipated, is the

* Carville and Duret "Sur les fonctions des Hêmisphéres Cérébraux," and Eckhard and Schwann, ("Hermann's Handbuch der Physiologie," 1878, Band ii. Th. 2. 132,) throw doubt on the existence of this *nodus cursorius*.

† "Journal de Physiologie," Band iii. 1823, p. 376.

‡ Longet, Op. cit. Schiff, "De vi motoriâ baseos Encephali," Bockenhemii, 1854; and Lafargue, "Essai sur la Valeur des Localisations Encéphaliques," &c., Thèse Inaug., Paris, 1838.

§ "Centralblatt," 1874, p. 513.

‖ Hitzig ("Centralblatt," 1874, p. 548) criticises Dr. Sanderson's statements.

annihilation of sensibility and of the power of voluntary movement in the body generally.* When, however, the Crura cerebri of a rabbit are not completely divided, but one of them is partially cut through a little in front of the Pons Varolii, the animal is said by Longet and Schiff to exhibit a constant tendency to turn towards the side opposite to that of the lesion, so that it performs the circular *évolution du manége ;* the diameter of its circle of movement being smaller in proportion as the incision approaches the edge of the Pons. But if one of the Crura be completely divided, the animal then falls over on the opposite side ; the limbs of that side being paralysed to the influence of the Encephalic centres, though they may be still caused to exhibit reflex motions. Hence it appears that the circular movements which are performed after incomplete lesions of the Crus cerebri and Thalamus opticus of either side, are due to the weakening of the sensori-motor apparatus of the opposite side, whereby the balance of the muscular actions of the two sides is destroyed. Nearly the same results have been obtained on this point by Longet, Lafargue, and Schiff. Afanasieff† found that in the course of two or three weeks an animal, in which one of the cerebral peduncles had been divided, was able to run straight forward. The section causes complete paralysis of the oculo-motorius on the same side, and imperfect paralysis of the facial nerve on the opposite side. Besides diminished sensibility of the body and head, it also produces contraction of the arteries, which lasts for 10 or 15 days, and is more marked in the ear of the *same* side. At the moment of section the blood pressure is increased, and the pulse retarded, and in half an hour the temperature of the body falls 3° F. Division of both peduncles destroys the power of voluntarily relaxing or constricting the sphincter ani, as well as of relaxing the constrictor urethræ.

484. Considerable importance is attached by some Physiologists to the part of the Encephalon known as the *Tuber annulare*, to which the name of *Mesocephaln* has also been given. This is not altogether synonymous with the *Pons Varolii*, as some Anatomists have represented it; for while the latter consists of transverse fibres which form the commissure between the hemispheres of the Cerebellum, surrounding and passing between the longitudinal fibres of the Sensory and Motor tracts which constitute the Crura cerebri, the Tuber annulare (which exists in animals whose Cerebellum has no hemispheres) is a projection from the surface of the proper Medulla oblongata, containing a considerable nucleus of vesicular matter. M. Brown-Séquard‡ has drawn the following conclusions respecting the functions of this part of the Encephalon, chiefly based on pathological evidence :—1. That the restiform bodies and their prolongations into the Pons, and into the Cerebellum, are not, as has been supposed, the conductors of sensory impressions. 2. That whilst hyperæsthesia occurs on the same side of the body when the Spinal cord is injured, especially in its posterior part, it appears on the opposite side of the body when a section is made either of the anterior or posterior surface of the Pons; and this he believes to favour his view of the decussation of the sensory fibres in the Cord, and to be opposed to the old view of the decussation of these

* It is considered by Longet that these functions are not *completely* destroyed, because the animals on whom this operation has been performed still retain some power of movement, and respond by cries to impressions that ordinarily produce pain. There is no proof, however, that such actions are other than 'excito-motor;' they certainly cannot in themselves be admitted as proving the persistence of consciousness in the lower segment of the Cerebro-Spinal axis. (See Brown-Séquard, "Central Nervous System," 1860, p. 225; and Schroeder v. d. Kolk, Syd. Soc. Trans., 1859, p. 76.)

† "Wien. Med. Wochensch.," pp. 137, 153, 169, and 185.

‡ "Journ. de la Physiol.," vol. i. p. 762; vol. ii. p. 121.

fibres below the Tubercula quadrigemina, or in the substance of the Pons itself. 3. The transmission of sensory impressions in the Pons appears to be chiefly effected by its central portion, whilst the anterior portion is chiefly instrumental in the conduction of the mandates of the Will to the Muscles. The experiments of Longet led him to the conclusion that the Tuber annulare, the structure of which is very complicated, is an independent centre of sensation and of motor power. He states that convulsive movements are excited by irritating it, and especially by the transmission of an electric current through its substance. These movements, according to Dr. Todd, appear to be of a different character from those which are excited by the application of the same stimulus to the Spinal cord and Medulla oblongata; for he states that while the convulsions excited by the transmission of an interrupted current through the parts just named, are *tetanic*, the muscles being thrown into a state of *fixed* contraction—those which ensue when the current is transmitted through the region of the Mesocephalon and Corpora quadrigemina, are *epileptic*, being combined movements of *alternate* contraction and relaxation, flexion and extension, affecting the muscles of all the limbs, of the trunk, and of the eyes, which roll about as in epilepsy.* Others† regard it as a centre for the automatic movements and muscular action required for locomotion and for standing, as well as for the perception of sensations of taste and of hearing.

485. The evidence afforded by Pathology regarding the functions of these Ganglionic masses is not altogether self-consistent; but this arises, probably, from the circumstance that the effects of morbid changes (particularly of sanguineous effusions) in any part of the Encephalon, extend themselves to other parts than those in which the obvious lesions are found; as is abundantly proved by the great variety of phenomena which present themselves as the results of lesions apparently similar, and by the similarity of the phenomena that are frequently consequent upon lesions of very different parts. It is established by abundant evidence that disease of the Corpora striata, or Thalami optici, or hæmorrhage into these bodies, produces hemiplegia, or paralysis of the opposite side. This paralysis, however, is not uniform, but affects chiefly the arm and leg, and in a less degree the face, whilst sensation is usually only slightly affected, or escapes altogether. An ingenious attempt has been made by Dr. Broadbent‡ to explain the phenomena observed in these cases. He observes that the relative situation of the two ganglia (Corpus striatum and Optic thalamus) will in some measure account for the circumstance that sensation so frequently escapes when motor power is lost; since the Corpus striatum—the motor ganglion—is in front of and external to the Thalamus, and may therefore easily be extensively damaged without involving the latter, or the fibres passing from it to the Cord. The Thalamus—the sensory ganglion—on the other hand, lying behind the Corpus striatum, and upon the fibres connecting it with the Cord, can scarcely be seriously affected without injury to those fibres or the Corpus striatum itself. Again, the Optic thalamus, according to hypothesis, standing with respect to the Corpus striatum in the relation of a sensory to a motor nerve-nucleus, it would almost follow that severe injury to the former would paralyze the latter by inhibitory influence, even when the injury was confined to the Thalamus, and did not reach the Corpus striatum directly or indirectly. Lastly, the experiments of M. Brown-Séquard may be referred to, as showing that, in the case of the Spinal cord, a very much more completed estruction of the grey matter is requisite

* Lumleian Lectures, 'On the Pathology and Treatment of Convulsive Diseases,' in "Medical Gazette," May 11, 1849. † Fort, "Physiologie Humaine," 1880, p. 63.
‡ "Med.-Chir. Rev.," April, 1866.

to destroy sensation entirely than is requisite for the abolition of the power of motion. Dr. Broadbent considers that the partial character of the paralysis may further be referred to the mode of functional activity of the muscles affected as compared with those which escape, and believes it may be shown that where the muscles of the corresponding parts on opposite sides of the body constantly act in concert, and seldom if ever independently, the nerve nuclei of these muscles are so connected by commissural fibres as to be *pro tanto* a single nucleus. This combined nucleus will have a set of fibres from each Corpus striatum, and will usually be called into action by both; but it will also be capable of being excited by either singly, though more or less completely according as the commissural connection between the two halves is more or less perfect. In support of this statement, it may be observed that those muscles which are commonly associated in their movements like the ocular muscles, are not paralyzed; those of the cheek, on the other hand, exhibit a degree of independence of action, and are slightly paralyzed; and lastly, the muscles of the arm and leg, which are almost completely independent in their action, are most severely affected. It is found also that in unilateral convulsion or spasm, the movements are bilateral in those parts which escape paralysis in Hemiplegia—*i.e.*, the combined nucleus transmits the irregular one-sided impulse along the nerves of both sides.

486. In employing the information derived from the foregoing sources as a guide in the inquiry into the part performed by the Sensory ganglia in the ordinary operations of the Cerebro-spinal system, we have to distinguish, as in the case of the Spinal Cord, between their operation as independent centres, and their action in subservience to the Cerebrum, which is superposed upon them.—We have seen reason to conclude that, in their former capacity, they are to be regarded as the true seat of *Sensation* (*i.e.* the material instruments through which the consciousness becomes affected by external impressions), and as the instrument, in virtue of their own 'reflex' power, of that class of Instinctive or Automatic movements, which require to be prompted and guided by sensations, and which cannot, therefore, be referred to the excito-motor group. But although it is sufficiently obvious that such movements constitute the highest manifestations of Animal life in the Invertebrata generally, and that they are but little modified by any higher principle of action even in the lower Vertebrata, yet it is no less obvious that in adult Man, in whom the Intelligence and Will are fully developed, we have comparatively little evidence of this independent reflex action of the Sensory ganglia:—all those automatic actions which are *immediately* necessary for the maintenance of his Organic life, being provided for by the excito-motor portion of the apparatus, so that although sensation ordinarily accompanies most of them, it is not essential to them; whilst those which are necessary to provide more *remotely* for its requirements, are for the most part committed to the guidance of his Reason. For the impressions which have been brought by the afferent nerves to his Sensorium, and which have there produced sensations, do not in general react at once upon the motor apparatus (as they do in those animals in which the Sensory ganglia are the *highest* of the nervous centres), but usually transmit their influence upwards to the Cerebrum, through whose instrumentality they give rise to ideas and reasoning processes, which operate upon the motor apparatus either emotionally or volitionally. And it is for the most part only when this upward transmission is checked, either by the non-development or the functional inactivity of the Cerebrum, or by its complete occupation in some other train of action—or, on the other hand, when the reflex action of the Sensory ganglia is called into play with unusual potency—

that we have any manifestations of the *sensori-motor* or *consensual* mode of operation in Man, that are at all comparable in variety or importance to those instinctive acts which are so remarkable in the lower animals.

487. Still, sufficient evidence of the existence of this class of reflex movements may be drawn from observation of the actions of Man in his ordinary condition; examples of it being furnished (as we have seen) by the closure of the eyes to a dazzling light, the start caused by a loud and unexpected sound, and the sneezing excited by sensory impressions on the Schneiderian membrane or on the Retina. To these may be added the vomiting produced by various sensory impressions, as the sight of a loathsome object, a disagreeable smell, a nauseous taste, or that peculiar feeling of want of support which gives rise to 'sea-sickness,' especially when combined with the sight of continually-shifting lines and surfaces, which itself in many individuals disposes to the same state; the involuntary laughter which is excited by tickling, and also that which sometimes bursts forth at the provocation of some sight or sound to which no ludicrous idea or emotion can be attached; the yawning which is excited by an internal sensation of uneasiness (usually arising from deficient respiration), or by the sight or sound of the act as performed by another; and those involuntary movements of the body and limbs, excited by uneasy sensations (probably muscular), which are commonly designated as 'the fidgets.' When the reflex activity of the Sensory ganglia is more strongly excited, in consequence either of an unusual potency of the sensory impressions, or of an unusual excitability of this part of the nervous centres, a much greater variety of sensori-motor actions is witnessed. The powerful involuntary contraction of the orbicularis and of the muscles which roll the eyeball upwards and inwards, in cases of excessive irritability of the retina is one of the best examples of this kind; but another very curious illustration is afforded by the involuntary abridgment of the excito-motor actions of respiration, when the performance of these is attended with pain—the dependence of this abridgment upon the direct stimulus of sensation, rather than upon voluntary restraint, being obvious from the fact that it often presents itself on *one* side only, a limitation which the Will cannot imitate. Again, there are certain Convulsive disorders which appear to depend upon an undue excitability of these centres, the paroxysms being excited by impressions which act through the organs of sense, and are not thus operative unless the patient be conscious of them; thus in Hydrophobia, we observe the immediate influence of the sight, sound, or contact, of liquids, or of the slightest currents of air, in exciting muscular contractions: and in many Hysteric subjects, the sight of a paroxysm in another individual is the most certain means of its induction in themselves. A remarkable case of this general exaltation of purely sensorial excitability has been recorded by Dr. Cowan, who gives the following account of its phenomena, which can scarcely be referred to any other than this category. "The shadow of a bird crossing the window, though the blind and bed-curtains are closed, the displacement of the smallest portion of the wick of a candle, the slightest change in the firelight, induce a sudden jerking of the spinal muscles, extending to the arms and legs when violent, and this without the slightest mental emotion of any kind beyond a consciousness of the movement. At times the vocal organs are implicated, and a slight cry, quite involuntary, takes place. At these periods the patient is unusually susceptible of all noises, especially the least expected and least familiar. Movements in the next house inaudible to others, the slightest rattle in the lock of a door, tearing a morsel

of paper, and a thousand little sources of sound not to be catalogued, induce results similar to those of visual impressions."*

488. It is, however, when the Cerebrum is not in a state which renders it capable of receiving and acting-upon Sensorial impressions, that we find the independent reflex activity of the Sensory ganglia most strikingly displayed. Thus, in the Infant for some time after its birth, it is obvious to an attentive observer, that a large part of its movements are directly prompted by sensations to which it can as yet attach no distinct ideas, and that they do not proceed from that *purposive* impulse which is essential to render them voluntary. This is well seen in the efforts which it makes to find the nipple with its lips; being probably guided thereto at first by the smell, but afterwards by the sight also; when the nipple has been found, the act of suction is purely excito-motor, as already explained. So in the Idiot whose brain has never attained its normal development, the influence of sensations in directly producing respondent movements is obvious to all who examine his actions with discrimination; and a remarkable case has been described,† in which an entire though temporary suspension of Cerebral power, reducing the subject of it to the condition of one of the lowest Vertebrata, gave a very satisfactory proof of the independent action of this division of the Encephalic centres.

489. But we do not require to go so far in search of characteristic examples of this kind of reflex action; since they are afforded by the performance of *habitual* movements, which are clearly under Sensorial guidance, when the Cerebrum is occupied in some train of action altogether disconnected with them. An individual who is subject to 'absence of mind,' may fall into a reverie whilst walking the streets; his attention may be entirely absorbed in a train of thought, and he may be utterly unconscious of any interruption in its continuity; and yet during the whole of that time his limbs shall have been in motion, carrying him along the accustomed path, whilst his vision shall have given to those movements the direction which is requisite to guide him along a particular line, or to move him out of it for the avoidance of obstacles. As already pointed-out there seems strong reason for regarding the ambulatory movements of the limbs as in themselves excito-motor; but the *guidance* of these movements by the visual sense indicates the participation of the Sensorium in this remarkable performance.—It has been maintained by some Metaphysicians and Physiologists, that these 'secondarily automatic' actions always continue to be voluntary, because their performance is originally due to a succession of volitional acts, and because, in any particular case, it is the Will which first excites them, whilst an exertion of the Will serves to check them at any time. But this doctrine involves the notion that the Will is in a state of pendulum-like oscillation between the train of thought and the train of movement; whereas nothing is more certain to the individual who is the subject of both, than that the former may be as uninterrupted as if the body were perfectly at rest, and his reverie were taking place in the quietude of his own study. And as it commonly happens that the direction taken is that in which the individual is most in the habit of walking, it will not unfrequently occur that if he had previously intended to pursue some other, he finds himself, when his reverie is at an end, in a locality which may be very remote from that towards which his walk was originally destined; which would not be the case, if his movements had been still under the purposive direction of the Will. And although it is perfectly true that these movements can be at any time checked by an effort of the will, yet this

* "Lancet," Oct. 4, 1845. † Ibid, Nov. 15 and 29, 1845.

does not really indicate that the will has been previously engaged in sustaining them; since, for the will to act upon them at all, the *attention* must be recalled to them, and the Cerebrum must be liberated from its previous self-occupation. And the gradual conversion of a volitional into an automatic train of movements, so that at last this train, once started, shall continue to run-down of itself, will be found to be less improbable than it would at first appear, when it comes to be understood that the mechanism of both sets of actions is essentially the same, and that they merely differ as regards the nature of the stimulus which originally excites them. That the same automatic movements are not excited by the same sensations, when the Cerebrum is in its ordinary state of functional connection with the Sensorium, is a fact entirely in harmony with the principle already laid-down. The complete occupation of the mind in other ways, as in close conversation or argument, or even (it may be) in the voluntary direction of some other train of muscular movements, is no less favourable than the state of reverie to that independent action of the Automatic centres which has been now described.

490. In the state of entire functional activity of the nervous centres of Man, however, there can be no doubt that the operation of the Sensory Ganglia is entirely subordinated to that of the Cerebrum; and that it furnishes an essential means of connection between the actions of the Cerebrum on the one hand, and those of the organs of Sense and Motion on the other, by the combination of which the Mind is brought into relation with the external world. For, in the first place, it may be affirmed with certainty that no mental action can be originally excited, save by the stimulus of Sensations; and it is the office of the Sensory ganglia to form these out of the impressions brought to them from the organs of sense, and to transmit such sensorial changes to the Cerebrum. But they have a no less important participation in the downward action of the Cerebrum upon the Motor apparatus; for no voluntary action can be performed without the assistance of a *guiding sensation*, as was first prominently stated by Sir C. Bell.*—In the majority of cases, the guiding or controlling sensation is derived from the muscles themselves, of whose condition we are rendered cognizant by the sensory nerves with which they are furnished; but there are certain cases in which it is ordinarily derived from one of the special senses, and in which the 'muscular sense' can only imperfectly supply the deficiency of such guidance; whilst, again, if the 'muscular sense' be deficient, one of the special senses may supply the requisite information. The proof of this necessity is furnished by the *entire impossibility of making or sustaining voluntary efforts, without a guiding sensation of some kind.* Thus, in complete anæsthesia of the lower extremities, without loss of muscular power, the patient is as completely unable to walk as if the motor nerves had also been paralyzed, unless the deficient sensorial guidance be replaced by some other; and in similar affections of the upper extremities, there is a like inability to raise the limb or to sustain a weight. But in such cases, the deficiency of the 'muscular sense' may be made good by the visual; thus, the patient who cannot feel either the contact of his foot with the ground, or the muscular effort he is making, can manage to stand and walk by *looking* at his limbs; and the woman who cannot feel the pressure of her child upon her arms, can yet sustain it so long as she keeps her eyes fixed upon it, but no longer—the muscles ceasing to contract, and the limb drooping powerless, the moment that the eyes are withdrawn from it. Thus it is, too, that when we are about to make a muscular effort,

* See his chapter 'On the Nervous Circle which connects the Voluntary Muscles with the Brain,' in his work, "On the Nervous System of the Human Body."

the amount of force which we put forth is governed by the mental conception of that which will be required, as indicated by the experience of former sensations; just as the contractions of the muscles of vocalization are regulated by the conception of the sound to be produced. Hence, if the weight be unknown to us, and it prove either much heavier or much lighter than was expected, we find that we have put forth too little or too great a muscular effort.

491. There are two groups of muscular actions, however, which, although no less voluntary in their character than the foregoing, are yet habitually guided by other sensations than those derived from the muscles themselves. These are, the movements of the *Eyeball*, and those of the *Vocal apparatus*.—The former are directed by the visual sense,* by which the action of the muscles is guided and controlled, in the same manner as that of other muscles is directed by their own 'muscular sense;' and hence it happens that, when we close our eyes, we cannot move them in any required direction without an effort that strongly calls-forth the muscular sense by which the action is then guided. In persons who have become blind after having once enjoyed sight, an association is formed by habit between the muscular sense and the contractile action, that enables the former to serve as the guide after the loss of the visual sense; but in those who are born *perfectly* blind, or who have become so in early infancy, this association is never formed, and the eyes of such persons exhibit a continual indeterminate movement, and cannot by any amount of effort be steadily fixed in one spot, or be turned in any definite direction. A very small amount of the visual sense, however, such as serves merely to indicate the direction of light, is sufficient for the government of the movements of the eyeball.—In the production of vocal sounds, again, that nice adjustment of the muscles of the Larynx, which is requisite to the giving forth of determinate tones, is ordinarily directed by the auditory sense: being learned in the first instance under the guidance of the sounds actually produced; but being subsequently effected voluntarily, in accordance with the mental conception (a sort of inward sensation) of the tone to be uttered, which conception cannot be formed, unless the sense of hearing has previously brought similar tones to the mind. Hence it is that persons who are born *deaf* are also *dumb*. They may have no malformation of the organs of speech; but they are incapable of uttering distinct vocal sounds or musical tones, because they have not the guiding conception, or recalled sensation, of the nature of these. By long training, however, and by imitative efforts directed by muscular sensations in the larynx itself, some persons thus circumstanced have acquired the power of speech; but the want of a sufficiently definite control over the vocal muscles is always very evident in their use of the organ.—It is very rarely that a person who has once enjoyed the sense of hearing, afterwards becomes so *completely* deaf, as to lose all auditory control over his vocal organs. An example of this kind, however, has been communicated to the public by a well-known author, as having occurred in himself; and the record of his experiences† contains many points of much interest. The deafness was the result of an accident occurring in childhood, which left him for some time in a state of extreme debility; and when he made the attempt to speak, it was with considerable pain in the vocal organs. This pain probably resulted from the unaccustomed effort which it was necessary to make, when the usual guidance was wanting; being analogous to the uneasiness which we experience, when we attempt to move our eyes with the lids closed. His

* See Dr. Alison's Memoir on the 'Anatomical and Physiological Inferences from the Study of the Nerves of the Orbit,' in "Trans. of Roy. Soc. of Edinb.," vol. xv.

† See the "Lost Senses," by Dr. Kitto, vol. i. chapters ii. and iii.

voice at that time is described as being very similar to that of a person born deaf-and-dumb, but who has been taught to speak. With the uneasiness in the use of the vocal organs, was associated an extreme mental indisposition to their employment; and thus, for some years, the voice was very little exercised. Circumstances afterwards forced it, however, into constant employment; and great improvement subsequently took place in the power of vocalization, evidently by attention to the indications of the muscular sense. It is a curious circumstance fully confirming this view, that the words which had been in use previously to the supervention of the deafness, were still pronounced (such of them, at least, as were kept in employment) as they had been in childhood; the muscular movements concerned in their articulation having still been guided by the original auditory conception, in spite of the knowledge derived from the information of others that such pronunciation was erroneous. On the other hand, all the words subsequently learned were pronounced according to their spelling; the required associations between the muscular sensations and the written signs being in this case the obvious guide.

492. It is through the 'muscular sense,' in combination with the visual and tactile, that those movements are regulated which are concerned alike in ordinary progression, and in the maintenance of the equilibrium of the body. That the visual sense has, in most persons, a large share in this regulation, is evident from the simple fact, that no one who has not been accustomed to the deprivation of it, can continue to walk straight-forwards, when blind-folded, or in absolute darkness, towards any point in the direction of which he may have been first guided. But the blind man, who has been accustomed to rely exclusively upon his muscular sense, has no difficulty in keeping to a straight path; and moves onwards with a confidence which is in remarkable contrast with the gait of a man who has been deprived of sight for the occasion only. In fact, as Mr. Mayo has well remarked,* in our ordinary movements, "we lean upon our eyesight as upon crutches."—When our vision, however, instead of aiding and guiding us, brings to the mind sensations of an antagonistic character, our movements become uncertain, from the loss of that power of guidance and control over them, which the harmony of the two sensations usually gives. Thus, a person unaccustomed to look down heights, *feels* insecure at the top of a tower or a precipice, although he *knows* that his body is properly supported; for the void which he sees below him contradicts (so to speak) the tactile sensations by which he is made conscious of the due equilibrium of his body. So, again, although any one can walk along a narrow plank, which forms part of the floor of a room, or which is elevated but a little above it, without the least difficulty, and even without any consciousness of effort, if that plank be laid across a chasm, the bottom of which is so far removed from the eye that the visual sense gives no assistance, even those who have braced their nerves against all emotional distraction, feel that an effort is requisite to maintain the equilibrium during their passage over it; that effort being aided by the withdrawal of the eyes from the abyss below, and the fixation of them upon a point beyond, which at the same time helps to give steadiness to the movements and distracts the mind from the sense of its danger. The degree in which the 'muscular sense' is alone sufficient for the guidance of such movements, when the mind has no consciousness of the danger, and when the visual sense neither affords aid nor contributes to distract the attention, is remarkably illustrated by the phenomena of Somnambulism; for the sleep-walker traverses, without the least hesitation, the narrow parapet of a house, and crosses narrow and insecure

* "Outlines of Physiology," 3rd edit., p. 345.

planks, clambers roofs, &c., under circumstances that clearly indicate the nature of the guidance by which he is directed.—The dependence of our ordinary power of maintaining our equilibrium, upon the combination of the guiding sensations derived through the sight and the touch, is further well illustrated, as Mr. Mayo has pointed out (loc. cit.), by what happens to a landsman on first going to sea. "It is long before the passenger acquires his 'sea legs.' At first, as the ship moves, he can hardly keep his feet; the shifting lines of the vessel and surface of the water unsettle his visual stability; the different inclinations of the planks he stands-on, his muscular sense. In a short time he learns to disregard the shifting images and changing motions, or acquires facility in adapting himself (like one on horseback) to the different alterations in the line of direction in his frame." And when a person who has thus learned by habit to maintain his equilibrium on a shifting surface, first treads upon firm ground, he feels himself almost as much at fault as he did when he first went to sea; and it is only after being some time on shore, that he is able to resume his original manner of walking. Indeed, most of those who spend the greater part of their time at sea, acquire a peculiar gait, which becomes so habitual to them that they are never able to throw it off.

493. But further, there is very strong physiological evidence that the Sensory ganglia are not merely the instruments whereby our voluntary movements are directed and controlled, in virtue of the guiding sensation which they furnish, but that they are actually the immediate centres of the motor influence which excites muscular contractions, in obedience to impulses transmitted downwards from the Cerebrum. It has usually been considered that the Cerebrum acts directly upon the muscles, in virtue of a direct continuity of nerve fibres from the grey matter of its convolutions, *through* the Corpora striata, the motor tract of the Medulla oblongata, the anterior portion of the Spinal cord, and the anterior roots of the nerves; and that in the performance of any voluntary movement, the Will determines the motor force to the muscle or set of muscles by whose instrumentality it may be produced. To this doctrine, however, the anatomical facts already stated constitute a very serious objection; for the motor tract cannot be stated with certainty to have any higher origin than the Corpora striata; and it is impossible to imagine that the fibres which converge towards the surface of these bodies from all parts of the Cerebrum, can be so closely compacted together as to be included in the motor columns of the Spinal axis. The fact would rather seem to be, that these converging fibres bear the same kind of anatomical relation to the Corpora striata and the other Sensorial centres of motor power, as do the fibres of the afferent nerves which proceed to them from the retina, the Schneiderian membrane, and the other peripheral expansions of nervous matter; and hence we might infer that the nerve-force generated in the convolutions, instead of acting *immediately* on the motor nerves, is first directed towards the Automatic centres, and excites the same kind of motor response in them, as would be given to an impression transmitted to them through a sensory nerve. We shall find that such a view of the structural arrangements of these parts is in remarkable accordance with their functional relations, as indicated by a careful analysis of the mechanism of what is commonly regarded as 'voluntary' movement. The Cerebrum may thus call the motor apparatus into action, as the instrument either of *ideas*, of *emotions*, or of *volitional determinations;* but we must limit our present examination to *voluntary* movements alone, these having been usually regarded as in such complete antagonism to those of the automatic group, that even separate sets of nerve-fibres have been thought requisite to account

for the transmission of these two distinct orders of motor impulses to the muscles.

494. Now, in the first place, it may be asserted, with some confidence, that no effort of the Will *can* exert that direct influence on the muscles which our ordinary phraseology, and even the language of scientific reasoners, would seem to imply; but, on the other hand, that the Will is solely concerned in determining the *result;* the selection and combination of muscular movements required to bring about this result, *not* being effected by the Will, but by some intermediate agency. If it were otherwise, we should be dependent upon anatomical knowledge for our power of performing the simplest movement of the body; whereas we find the fact to be, that the man who has not the least idea of the mechanism of muscular action, can acquire as complete a command over his movements, and can adapt them as perfectly to the desired end, as the most accomplished anatomist could do. Further, we cannot, by any exertion of the Will, single out a particular muscle, and throw it into contraction by itself, unless that muscle be one which is alone concerned in an action that we can voluntarily perform; and even then we single it out by *willing* the action. Thus we can put the *levator palpebræ* in action by itself; but this we do, not by any conscious determination of power to the muscle itself, but by *willing* to raise the eyelids; and it is only by our anatomical knowledge that we know that but a single muscle is concerned in this movement. So far as our own consciousness can inform us, there is no difference between the mechanism of this action and that of the flexion of the knee- or elbow-joint; and yet in these latter movements several muscles are concerned, not one of which can be singled-out by any effort of the will, and thrown into action separately from the rest.—The idea that the Will is *directly* exerted upon the muscles called into action to produce a particular movement, may seem to derive some support from the sense of *muscular effort* of which we are conscious in making the exertion, and which we refer to the muscles which are concerned in it; but this sense of effort is nothing else than the 'muscular sense' already alluded to, which has its origin in the state of tension of the muscles, and which is no more an indication of *mental* effort directed to them, than the sensation of light or sound is an indication of a determination of voluntary power to the eyes or ears.

495. There are two cases, already referred to under another head, in which it is very easy to show that the Will is concerned with the result alone, and is not directly exerted upon the instruments by which that result is brought about: these are, the movements of the eyes, and the production of vocal tones. In neither of them are we conscious of any effort in the muscular apparatus, unless the contraction be carried beyond its accustomed extent; the ordinary movements being governed, as already remarked, not by the muscular sense, but by the visual and auditory senses respectively.—Nothing can be more simple, to all appearance, than the act of turning the eyes upwards or downwards, to one side or the other, in obedience to a determination of the Will; and yet the Will does not impress such a determination upon the muscles. That which the Will really does, is to cause the eyeballs to roll in a given direction, in accordance with a visual sensation; and it is only *when there is an object* towards which the eyes can be turned that we can move them with our usual facility. When the eyelids are closed, and we attempt to roll the globes upwards or downwards, to one side or to the other, we feel that we can do so but very imperfectly, and with a sense of effort referred to the muscles themselves—this sense being the result of the state of tension in which the muscles are placed by the effort to move the eyes without the guiding visual

sensation. Now, on the other hand, the Will may determine to fix the eyes upon an object; and yet this very fixation may be only attainable by a muscular movement, which movement is directly excited by the visual sense, without any exertion of voluntary power over the muscles. Such is the case when we determinedly look steadily at an object, while we move the head horizontally from side to side; for the eyeballs will then be moved in the contrary direction by a kind of instinctive effort of the external and internal recti, which tends to keep the retinæ in their first position, and to prevent the motion of the images over them. So, when we look steadily at an object, and incline the head towards either shoulder, the eyeballs are rotated upon their antero-posterior axis (probably by the agency of the oblique muscles) apparently with the very same purpose—that of preventing the images from moving over the retinæ (see CHAP. XV., sect. 3). Now we cannot refuse to this rotation any of the attributes which really characterize the so-called voluntary movements; and yet we are not even informed by our own consciousness that such a movement is taking place, but know it only by observation of others, or by the reflection in a mirror.

496. The muscular contractions which are concerned in the production of vocal tones, are, in like manner, always accounted voluntary; and yet it is easy to show that the Will has no direct power over the muscles of the larynx. For we cannot raise or depress the larynx as a whole, nor move the thyroid cartilage upon the cricoid, nor separate or approximate the arytenoid cartilages, nor extend or relax the vocal ligaments, by simply *willing* to do so, however strongly. Yet we can readily do any or all these things by an act of the Will exerted for a specific purpose. We conceive of a tone *to be* produced, and we *will* to produce it; a certain combination of the muscular actions of the larynx then takes place, in most exact accordance with one another; and the predetermined tone is the result. This anticipated or conceived sensation is the guide to the muscular movements, when as yet the utterance of the voice has not taken place; but whilst we are in the act of speaking or singing, the contractile actions are regulated by the present sensations derived from the sounds as they are produced.—It can scarcely but be admitted, then, that the Will does *not* directly govern the movements of the larynx; but that these movements are immediately dependent upon some other agency.

497. Now what is true of the two preceding classes of actions is equally true of all the rest of the so-called *voluntary* movements; for in each of them the power of the Will is really limited to the determination of the result; and the production of that result is entirely dependent upon the concurrence of a 'guiding sensation,' which is usually furnished by the very muscles that are called into action. It is obvious, therefore, that we have to seek for some intermediate agency, which *executes* the actions *determined* by the Will; and when the facts and probabilities already stated are duly considered, they tend strongly in favour of the idea that even voluntary movements are executed by the instrumentality of the automatic apparatus, and that they differ only from the automatic or instinctive in the nature of the stimulus by which they are excited—the determination of the Will here replacing, as the *exciting cause* of its action, the sensory impression which operates as such in the case of an instinctive movement, and which is still requisite for its guidance.

498. This view of the case derives a remarkable confirmation from the analysis of two classes of very familiar phenomena: the first consisting of cases in which movements that are ordinarily Automatic are performed by Voluntary determination, or simply in respondence to an Idea; the second consisting of those in which movements originally Voluntary come by habit

to be Automatically performed.—Of the first class, the act of Coughing is a good example. This action, which is ordinarily automatic, may also be excited by a voluntary determination; such a determination, however, is directed to the *result*, rather than exercised in singling-out the different movements and then combining them in the necessary sequence; and the Will thus seems obviously to take the place of the laryngeal or tracheal irritation, as the *primum mobile* of the series, which, in its actual performance, is as automatic in the latter case as in the former. So, again, we know that many of the automatic movements which have been already referred-to as examples of the sensori-motor group (§ 487), and which the Will cannot call-forth, may be performed in respondence to *ideas* or *conceptions*, which are Cerebral states that seem to recall the same condition of the Sensorium as that which was originally excited by the Sensory impression. Thus it is well known that the act of Vomiting may be induced by the *remembrance* of some loathsome object or nauseous taste, excited by some act of 'suggestion;' and the Author has known an instance in which a violent fit of sea-sickness was brought-on by the sight of a vessel tossed about at sea, which recalled the former experience of that state. So the Hydrophobic paroxysm may be excited by the mention of the *name* of water, which of course calls up the idea; and a tendency to yawn is in like manner frequently induced by looking at a picture of yawners, or by speaking of the act, or by voluntarily commencing the act which may then be automatically completed. The automatic performance of actions which were originally voluntary has already been fully discussed (§489); and we have therefore only to remark here, that the fact very strongly supports the view now advanced, as to the *singleness* of the mechanism which serves as the instrument of both classes of actions, and the essential uniformity of its operation in the two cases.—It would be difficult to explain either set of phenomena satisfactorily, on the hypothesis that there is a 'distinct system' of fibres for the volitional and for the automatic movements; since it is not readily to be conceived how a set of movements originally performed by the one can ever be transferred to the other; whilst, on the other hand, it is easy to understand how the same motorial action may be excited in the automatic centres, either by an *external* impression conveyed thither by an afferent nerve from a sensory surface (as that of the irritation in the air-passages, which excites the act of coughing), or by a stimulus proceeding from the convoluted surface of the Cerebellum, and conveyed along those connecting fibres which Reil with great sagacity termed the 'nerves of the *internal* senses.'

499. To sum-up, then, we seem justified in concluding that the *Cranio-spinal axis* of Man and other Vertebrata—consisting of the Sensory ganglia, Medulla oblongata, and Spinal cord—is (like the chain of cephalic and ventral ganglia of Arthropoda with which it is homologous) the immediate instrument of *all sensorial and motor changes:* that by its sole and independent action are produced all those movements which are ranked as *automatic* or *instinctive*, these being performed in respondence to external impressions which may or may not affect the consciousness; but that when acting in subordination to the Cerebrum, the Cranio-spinal axis transmits upwards to it the influence of Sensorial changes, and receives from it the downward impulses, which it directs automatically into the appropriate channel for the execution of the movements which the mind has directed. The number of purely-automatic actions diminishes in proportion to the development of the Cerebrum, and to the subjection of the Automatic apparatus to its control; but even in Man, those most closely connected with the maintenance of the organic functions, or most necessary for the conservation of the bodily structure, remain

quite independent of any mental agency, and most of them do not require consciousness for their excitation. But if the activity of the Cerebrum be suspended or be otherwise directed, without any affection of the automatic apparatus, movements which have long been habitually performed in a particular sequence, may be kept-up, when the will has once set them in action, through the automatic mechanism alone; the impressional or sensational change produced by each action, supplying the stimulus which calls forth the next.—It may further be concluded that the Sensory ganglia, which are the instruments whereby we are rendered *conscious* of external impressions, are also the seat of those simple *feelings* of pleasure and pain which are immediately linked-on to that consciousness; for it can scarcely be doubted that such feelings must be associated with particular sensations, in animals that have no ganglionic centres above these; since we must otherwise regard the whole series of the Invertebrata as neither susceptible of enjoyment, nor capable of feeling pain or discomfort. And it likewise seems probable that the Sensory ganglia are also the seat of those *perceptional* acts which bring the consciousness into direct relation with the external object that aroused the sensation; since the recognition of *externality* seems evident in the actions of the tribes just referred to.* A few remarks may here perhaps appropriately be introduced, indicating the effects of lesion of the several ganglia at the base of the brain from above downwards. In the event of lesion, as hæmorrhage, occurring in front of or above the Corpora striata, no paralysis either motor or sensory is observed unless the damage be very great. The intellectual faculties are probably always more or less affected, though it may not be easy to determine in what mode or to what degree. As will subsequently be shown, if the posterior frontal convolutions, especially of the left side, be affected, aphasia is likely to occur. If the hæmorrhage occur in the Corpus striatum, there is *motor* paralysis of the opposite side only. If in the Thalamus opticus there would be motor paralysis of the opposite side, with more or less paralysis of sensation. If in the Crus cerebri there would be paralysis of the opposite side, which might be either motor or sensory, or both; and if the muscles of the eye be paralysed, it is on the same side, and would chiefly affect those supplied by the third. If in the Pons, there would be paralysis of motion or of sensation, or of both, of the opposite side of the body and the same side of the face—in those muscles mainly supplied by the 5th and 7th, that is—there would be crossed paralysis. If in the Medulla oblongata, the great centres of respiration, deglutition, &c., would be affected, and a fatal issue soon occurs.

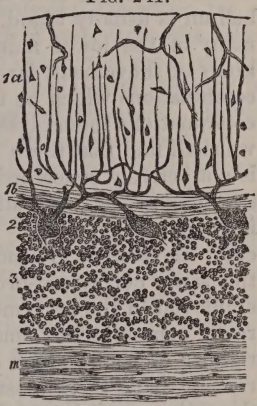
4. *Of the Cerebellum, and its Functions.*

500. The Cerebellum is an organ which, though confined to the Vertebrate Sub-Kingdom, is yet in peculiarly intimate relation with the Automatic apparatus. In that highest state of development which it presents in Man, we find it to consist of two *lateral* lobes or *hemispheres*, composed of nerve-fibres invested in a very peculiar manner by vesicular substance, and of a *central* lobe, also containing a combination of the vesicular and fibrous substances, which is known under the designation of the 'vermiform process.' The hemispheres are connected with each other not only by this central lobe, but also by the fibrous commissure which passes beneath the Medulla oblongata, and is known as the 'Pons Varolii.' The commissural fibres form part of the 'Crura cerebelli;' but another portion is formed by the strands which

* It may here be remarked that the term Sensation is now understood to imply the simple consciousness of an impression, whilst Perception refers that impression to something out of the *ego*. For the production of a Sensation a conscious state of the mind is all that is required; but for the exercise of the Perceptive power a certain degree of *attention* is requisite.

connect the Cerebellum with the anterior and posterior columns of the Spinal cord and Medulla oblongata; and, in addition to these, we find a fasciculus of fibres passing between the Cerebellum and the Corpora quadrigemina, the 'iter a cerebello ad testes.' The peduncle of its hemispheres on either side contains a mass of grey matter, the 'corpus rhomboideum,' or, 'dentatum,' which seems to be a ganglionic centre for the fibres that pass upwards to it from the Spinal cord. There are, then, three masses of grey matter in the cerebellum—that of the cortex, the dentated nuclei and the roof-nuclei of Stilling, situated in the medulla of the Vermiform process. The accompanying figure (Fig. 241) exhibits the appearance presented when a section of the cortex of the Cerebellum is examined, and it will be seen that it differs considerably from that of the Cerebrum given on p. 662.* The inquiries of Engel† have shown that the development of the Cerebellum is completed in infancy, and remains unaltered up to the 50th year, after which the number of the lamellæ, especially of the superior vermiform process, begins to diminish.

Fig. 241.



Section from the cortex of the Cerebellum of Man.
1 *a*. External portion of the pure grey layer.
1 *b*. Internal portion of the pure grey layer with fusiform cells and fibræ arcuatæ.
2. The layer of Purkinje's cells.
3. The layer of granules.
m. Medullary lamina.

501. When we examine into the relative development of the Cerebellum in the different classes of Vertebrata, we find that it presents some very remarkable differences.‡ In its simpler forms, this organ is found to consist entirely of the representative of the *central* lobe of the Human Cerebellum, the hemispheres not making their appearance until we have ascended to the class of Birds. On ascending the scale of Mammiferous animals, on the other hand, we cannot but be struck with the rapid advance in the proportional size of the Cerebellum, which we observe as we rise from the lowest (which are surpassed in this respect by many Birds), towards Man, in whom it attains a development which appears enormous, even when contrasted with that of the Quadrumana. In proportion, in fact, as the extremities acquire the power of prehension, and together with this a power of application to a great variety of purposes—still more, in proportion as the animal becomes capable of maintaining the erect posture, in which a constant muscular exertion, consisting of a number of most elaborately-combined actions, is required—do we find the size of the Cerebellum, and the complexity of its structure, undergoing a rapid increase. Thus, even between the Dog and Bear there is a marked difference; the latter being capable of remaining for some time in the erect posture, and often spontaneously assuming it; whilst to the former it is anything but natural. In the semi-erect Apes, again, there is a very great advance in the proportional size of the Cerebellum; and those which most approach Man in the tendency to preserve habitually the erect posture also come nearest to him in the dimensions of this organ.—Thus on looking at the

* For an admirable description of the Human Cerebellum, see Stilling's Essay on the Structure of the Organ. Cassel, 1867. Also Deiter's "Untersuch. üb. Gehirn. u. Rückenmark," 1865; Meynert, in Stricker's "Hum. and Comp. Histology," vol. ii. 1872, p. 512; Hadlich, "Archiv f. Microscop. Anat.," Band vi. p. 191.

† "Wien. Medizin. Wochens.," 1863, No. 33.

‡ See "Princ. of Comp. Phys., § 635.—Fuller information on this point will be found in M. Serres' "Anat. Comp. du Cerveau," and M. Leuret's "Anat. Comp. du Système Nerveux." —For a general discussion of the evidence afforded by Comparative Anatomy in regard to the functions of the Cerebellum, see the "Brit. and For. Med. Rev.," vol. xxii. pp. 535–541.

size of the Cerebellum, in relation to the general motor activity of the Vertebrate classes respectively, and especially taking into account the *variety* of their respective movements, and the number of separate muscular actions which are combined in each, we can scarcely help noticing that it is in the tribes which are most distinguished in these respects, that the largest Cerebellum is usually found. Now it is evident that Man, although far inferior to many of the lower animals in the power of performing various particular kinds of movement, far surpasses them all in the number and variety of the combinations which he is capable of executing, and in the complexity of the combinations themselves. Thus, if we attentively consider the act of *walking*, we shall find that there is scarcely a muscle of the trunk or extremities which is not actively concerned in it; some being engaged in performing the necessary movements, and others in maintaining the equilibrium of the body which is disturbed by them. On the other hand, in the Horse or Camel, the muscular movements are individually numerous, but they do not require nearly the same perfect co-ordination. And in the Bird, the number of muscles employed in the movements of flight, and in directing the course of these, is really comparatively small; as may at once be perceived, by comparing the rigidity of the skeleton of the trunk of the Bird with that of Man, and by remembering the almost complete inactivity of the lower extremities during the active condition of the upper. In fact, the motions of the wings are so simple and regular, as to suggest the idea, that, as in Insects, their character is more reflex than voluntary:—an idea which is supported by the length of time during which they can be kept up without apparent fatigue, and also by the important facts which experimental research has disclosed.

502. We have next to inquire what evidence can be drawn from Experimental investigations on the same subject; and in reference to this it is desirable to remark, in the first place, that the experimental mode of inquiry is perhaps more applicable to this organ than to other parts of the Encephalon; inasmuch as it can be altogether removed with little disturbance of the actions immediately essential to life, the animals soon recovering from the shock of the operation, and seeming but little affected except in some easily recognized particulars.* It is not to be expected that there should be an exact conformity among the results obtained by all experimenters. Everyone who has been engaged in physiological experiments is aware of the amount of difference caused by very minute variations in their circumstances; in no department of inquiry is this more the case than in regard to the Nervous System; and such differences are yet more likely to occur in experiments made upon its centres than in those which concern its trunks.—The investigations of Flourens† seem the most clear and decisive in their results; and of these we shall accordingly take a general survey. He found that, when the Cerebellum was mechanically injured, the animals gave no signs of sensibility, nor were they affected with convulsions. When the Cerebellum was being removed by successive slices, the animals became restless, and their movements were irregular; and by the time the last portion of the organ was cut away, the animals had entirely lost the power of springing, flying, walking, standing, and preserving their equilibrium—in short, of performing any combined muscular movements, which are not of a simply reflex character. When an animal in this state was laid upon the back, it could not recover its former posture; but it fluttered its wings and did not lie in a state of stupor. When placed in the erect

* The principal experimenters upon this subject have been Rolando, Flourens, Magendie, Hertwig, Longet, Schiff, Brown-Séquard, Wagner, Hitzig, and Ferrier.

† "Récherches Expérim. sur les Propriétés et les Fonctions du Système Nerveux."

position, it staggered and fell like a drunken man—not, however, without making efforts to maintain its balance. When threatened with a blow, it evidently saw it, and endeavoured to avoid it. It did not seem that the animal had in any degree lost voluntary power over its several muscles; nor did sensation appear to be impaired. The faculty of *combining* the actions of the muscles in groups, however, was completely destroyed; except so far as those actions (like that of Respiration) were dependent only upon the reflex function of the Spinal cord. The experiments afforded the same results, when made upon each class of Vertebrate animals.* The results obtained by other observers are not quite in accordance with those of Flourens. Dalton and Weir Mitchell found that in pigeons from which the greater part or the whole of the Cerebellum had been removed, and which survived the immediate effects of the operation, recovery took place after the lapse of some months, so far that the animal only exhibited feebleness and incapacity for prolonged muscular exertion, but no real want of co-ordination or unsteadiness of equilibrium. Experiments of this kind made on Mammals are attended with so much injury as to prove invariably fatal; but Combetti† has recorded a case of congenital absence of the Cerebellum in a girl who could stand and walk up to a short period before her death, but who was noticed to fall frequently. Wagner found that the chief symptoms produced in Pigeons from which he had removed the whole or the greater part of the Cerebellum were—1. A remarkable tendency on the part of the animal to throw itself on one side, and to keep the legs completely extended, with an indisposition to move them, though it was still evidently capable of flexing them by an effort of the will. 2. Torsion of the head on the neck. 3. Persistent trembling of the muscles of the body generally, resembling *paralysis agitans*. 4. Vomiting frequently accompanied by liquid alvine evacuations; and 5. The animals became thinner, the feathers fell off, and the temperature was much depressed. No symptoms were observed having reference to the generative organs. The perception of sensations and the performance of psychical operations appeared to be perfect; and though the voluntary control over the muscles was somewhat impaired, it was manifestly not altogether lost. Ferrier‡ notes that when the Cerebellum is divided exactly in the middle line in an antero-posterior direction, the disturbances of equilibrium, if any, are of no marked importance, and there is none of the tendency to reeling or rotation which characterizes undefined lesion of the organ. Injury of the anterior part of the middle lobe of the Cerebellum is followed, in the monkey, by a tendency to fall forwards, whilst after lesion of the posterior part there is a tendency to fall backwards, and this last disposition is observed in cases of disease of the middle lobe. Lussana observes that the results of irritation of the Cerebellum are usually vomiting, cephalalgia, convulsions, and affections of the pupil, strabismus, amblyopia, &c.; and he believes that in every case of extensive disease of the Cerebellum there are concurrent symptoms of disorder of the muscular movements, indicative of defect or absence of the "muscular sense."

503. It was further affirmed by Magendie, that the removal of the Cerebellum, or the infliction of a deep wound in its substance on both sides, occasions the animal to move *backwards* as if by an irresistible impulse,

* They have been since repeated, with nearly corresponding effects, by Bouillaud, Hertwig, and by many other experimenters. See Wagner, in Brown-Séquard's "Journal de la Physiol.," 1861, pp. 225 and 404; Lussana in idem, 1862, p. 418, 1863, p. 170; MM. Leven and Ollivier, "Archiv. Gén. de Méd.," Nov. and Dec. 1862; Dalton, "American Journal of Med. Science," 1861, vol. xli. p 83; Brown-Séquard, "Central Nervous System," 1860; Vulpian, "Leçons sur la Physiologie du Système Nerveux," 1866; Ferrier, "The Functions of the Brain," 1876, p. 85. † "Révue Médicale," 1831. ‡ Loc. cit., p. 93.

and this he attributed to the retrograde power of the Corpora striata, which now acts without its due balance. That such a movement does *sometimes* present itself after such injuries as have been described, cannot be questioned, the fact having been confirmed by other experimenters; but it is a phenomenon of such rarity, that it cannot be rightly considered as having any direct dependence upon the injury of the Cerebellum, but must be rather set-down to some accidental complication or concurrent disturbance; more especially since, as already pointed out, the function attributed by Magendie to the Corpora striata has no real existence.—But the results of section of one of the Crura cerebelli, which were first obtained by Magendie, are much more constant; for the performance of this operation causes the animal to fall-over upon one side, and to continue *rolling upon its longitudinal axis*, even as fast (in some instances) as sixty times in a minute, the movement going on for many days without intermission. The rotation is accompanied by a remarkable deviation of the eyes. The eye on the side of the lesion looks downwards and inwards, while the eye of the sound side looks upwards and backwards. There is a remarkable difference in the statements of different experimenters, however, as regards the direction of this rolling movement; for whilst Magendie and Müller affirm that it takes place *towards* the injured side, Longet and Lafargue assert that it takes place *from* the injured side towards the opposite side. This discrepancy appears, from the experiments of Schiff,* to be due to a difference in the locality of the section; for he states that if the peduncle be divided from *behind*, the animal turns *towards* the side in which the section is made; whilst if the section be made *in front*, the animal turns *from* that side towards the opposite one. The difference is explained by Longet, by the difference in the course of the anterior and posterior fibres of the peduncles: for, according to him, the former communicate with the decussating, and the latter with the non-decussating portion of the motor tract; so that, when the former are injured, the animal loses control over the muscles of the opposite side, and when the latter, over the muscles of the same side. This rolling movement is attributed by some to the continued activity of the muscles on one side, now unbalanced by that of the muscles on the other; but if such were the case, as Longet justly remarks, it ought to occur more frequently than it does in cases of ordinary hemiplegia; and, according to that experimenter, observation shows that it rather depends on a *twisting* movement of the muscles attached to the spinal column, especially affecting its anterior portion, and dragging the posterior (as it were) after it.† Thus M. Brown-Séquard,‡ who has shown that similar rolling movements may be produced by lesions of other parts of the nervous centres, as the Spinal cord, Medulla oblongata, and Pons, observes that the movements do not resemble those effected by voluntary muscles; but that, in consequence of the tonic contraction into which some muscles are thrown, the trunk and neck of the animal are twisted as far as the bones will permit, into the form of a corkscrew. He attributes the phenomena in question, which the animal evidently endeavours to check, to the irritation of a peculiar set of nerve-fibres not usually employed by the will, the division of which does not cause paralysis, though they may serve as the conductors of powerful motor impulses to special groups of muscles. MM. Leven and Ollivier, operating on guinea-pigs, found that puncture of the Cerebellum produced well-marked movements of rotation, usually proceeding from the side injured

* "De vi motoriâ baseos Encephali inquisitiones experimentales," Bockenhemii, 1845.

† See his "Traité de Physiologie," tom. ii. p. 408, 1860.

‡ "Central Nervous System," 1860, p. 193.

towards the opposite side. They did not observe any disorders of the alimentary canal similar to those noticed by Wagner and others, after ablation of portions of the Cerebellum. In his experiments on the effects of electrical stimulation of the Cerebellum in Monkeys, Ferrier found that irritation of the pyramid of the median lobe caused both eyes to turn to the side on which the stimulus was applied. Irritation of the posterior part of the upper vermiform process caused both eyes to look straight downwards. Irritation of the left side of the superior vermiform process (*declive monticuli*) caused both eyes to move downwards and to the left; irritation of the right side, downwards and to the right. Proceeding still further forwards, stimulation of the anterior extremity of the superior vermiform process in the middle line caused both eyes to move directly upwards; stimulation on the left side, both eyes upwards and to the left, without rotation; stimulation on the right side, both eyes upwards and to the right, without rotation. Stimulation of the lateral lobe on the left side caused both eyes to move upwards and to rotate to the left; on the right side it caused both to move upwards and to rotate to the right. Stimulation of the flocculus caused both eyes to rotate on their antero-posterior axes. Besides these ocular movements, certain movements of the head and limbs were produced, the movements of the head coinciding generally in direction with those of the eyes.*

504. The information supplied by Pathological phenomena, when interpreted with the cautions formerly referred to, is found on the whole to coincide with that obtained from experiment. In the first place, it fully supports the conclusion, that the Cerebellum is not in any way the instrument of *psychical* operations. Inflammation of the membranes covering it, if confined to that part, does not produce delirium; and its almost complete destruction by gradual softening does not appear necessarily to involve loss of intellectual power. "But," remarks Andral, "whilst the changes of intelligence were variable, inconstant, and of little importance, the lesions of motion, on the contrary, were observed in all the cases [of softening] except one; and in this it is not quite certain that motion was not interfered with." Yet the result of Andral's analysis of as many as ninety-three cases of disease of the Cerebellum,† is not favourable to the doctrine to which the results of experiments seem to point; but, as it has been justly remarked by Longet, the effects of disease are only partly comparable to those of experiment; since in a large proportion of chronic disorders, the changes consist in the formation of a new product, such as a tubercular or cancerous deposit, or a cyst of some kind, the gradual development of which is quite consistent with the continued functional activity of the organ, as we see by parallel phenomena elsewhere; whilst in those instances in which hæmorrhage occurs, this usually occasions either complete apoplexy or local paralysis, by its effects upon other organs. Still, several cases of chronic disease of the Cerebellum have been observed, in which *unsteadiness of gait*, without paralysis, or only giving place to paralysis at last on the occurrence of hæmorrhage, was a very marked symptom;‡ and these afford a strong confirmation of the doctrine based on the experimental researches already referred to. In a few cases in which both lobes of the Cerebellum have been seriously affected, the tendency to retrograde movement has been observed; and instances are also on record of the occurrence of

* The observations made by Hitzig, loc. cit., are very similar to those made by Ferrier.

† See his "Clinique Médicale," 2ème édit. tom. v. p. 735.

‡ Two such cases are recorded by Mr. Dunn in the "Med.-Chir. Trans.," vol. xxxii., and another by Dr. Cowan in the "Prov. Med. and Surg. Journ.," April 16, 1845; and the Author has been made acquainted with several others, by gentlemen under whose cognizance they have fallen. See also various papers by Hughlings Jackson in "Med. Times and Gazette."

rotatory movement, which has been found to be connected with lesion of the Crus cerebelli on the same side.* So far as they can be relied on, therefore, the results of the three methods of investigation bear a very close correspondence, and lead to the conclusion well expressed by Ferrier, that the Cerebellum is a complex arrangement of individually differentiated centres, which in associated action regulate the various muscular adjustments necessary to maintain the equilibrium of the body; each tendency to the displacement of the equilibrium round a horizontal, vertical, or intermediate axis acting as a stimulus to the special centre which calls into play the antagonistic or compulsory action.

505. It must not be allowed to pass unnoticed, that some Physiologists (as Foville, Pinel-Grandchamp, and Dugès) have regarded the Cerebellum as the centre of common sensation; chiefly on the ground of its connection with the posterior columns of the Spinal cord, and of the manifestations of pain which are called-forth by touching the Restiform columns. Although these facts may lead us to admit that the Cerebellum is connected with the sensorial centres, and even that it is itself *a* seat of sensibility, yet it is impossible to regard it as the exclusive seat of sensibility, consistently with the facts with which experiment and pathological observation supply us; since neither the removal of the entire organ by operation, nor its complete destruction by disease,† has been found to involve any loss of the ordinary sensorial powers. —There would seem much more probability in the idea, that it is the special seat of the "muscular sense," which has so important a share in the guidance of the co-ordinated movements (§ 492); and this notion derives confirmation from the marked structural connection which exists between the Cerebellum and the Optic ganglia (corpora quadrigemina), the purpose of which may be not unfairly surmised to be, to communicate the guidance of the *visual* sense to the organ by which the co-ordination of motions is effected, in the same manner as the impressions appertaining to the 'muscular sense' are transmitted upwards by the Restiform columns.‡ The chief objection to such a view, would seem to lie in the strong similarity between the 'muscular' sense and 'common' or 'tactile' sensation, which makes it difficult to conceive that they should have different seats in the *Sensorium commune*. But this difficulty is diminished if not removed by the reflection, that the Restiform columns appear to have the same endowments as the remainder of the Sensory tract derived from the posterior columns of the Spinal cord; and that no explanation can be given of their extreme sensitiveness to impressions (as shown by experiment), unless it be admitted that the organ in which they terminate is itself a centre of a form of sensation closely allied to that of the common or tactile kind. Possibly, however, the true termination of these fibres is in the 'corpus dentatum' of the Crura cerebelli; and the Cerebellum may react upon impressions thence transmitted to it, without being itself the instrument of communicating such impressions to the consciousness.§ Dr.

* A collection of such cases has been made by Dr. Paget, in his Paper on 'Morbid Rhythmical Movements,' in the "Edinb. Med. and Surg. Journal," 1847, vol. lxvii.—A case once fell within the Author's knowledge, in which a state of this kind, that lasted for some hours, appeared to depend upon an attack of Indigestion; the symptoms being completely relieved by vomiting, and no further indication of Encephalic disorder manifesting itself.

† See the well-known case recorded by Combetti, in the "Revue Médicale," t. ii. p. 57.

‡ This view, suggested many years since by the Author, has been recently supported in the able papers by M. Ph. Lussana in the "Journal de la Physiologie," tom. v. 1862, p. 484, and tom. vi. p. 169; and also by Mr. Robert Dunn, in his "Essay on Physiological Psychology" (London, 1858), who also places the centre of the muscular sense in the corpus rhomboidale of the Cerebellum.

§ M. Brown-Séquard ("Journ. de la Physiol.," vol. i. 1858, p. 535) and Wagner (Op. cit.)

Laycock* states that the consideration of a large and varied series of facts have led him to the conclusion that the Cerebellum with its connection downwards along the medulla oblonganta and spinal cord, and upwards into the hemispheres, is the great trophic centre. This centre may be excited to functional activity, not only by afferent impressions from the body, whether consciousness be coincident or not, but also by afferent impressions from the vast periphery of the cerebral hemispheres, and in this case also whether consciousness be coincident or not; in short, that the cerebral hemispheres are not functionally restricted to intellectual processes, as is generally held, nor the cerebellum to muscular co-ordination, but that both conjointly influence the whole of the organic processes.

506. We have now to examine, however, another doctrine regarding the functions of the Cerebellum, which was first propounded by Gall, and which is supported by the Phrenological school of physiologists. This doctrine, that the Cerebellum is the organ of the sexual instinct, is not altogether incompatible with the other; and by some it has been held in combination with it. The greater number of Phrenologists, however, regard this instinct as the *exclusive* function of the Cerebellum; and assert that they can judge of its intensity by the degree of development of the organ. We shall now examine the evidence in support of this position, afforded by the three methods of inquiry which have been already indicated.—In the first place it may be remarked, that the sexual propensity is very closely connected with various emotional states of mind, to which 'organs' are assigned by Phrenologists, and of which the Cerebellum is universally admitted to be the seat; such for instance as 'love of offspring,' 'adhesiveness,' and (in the lower animals more particularly) 'combativeness;' whilst in man it has a continual operation upon the reasoning faculties and the will. Yet the anatomical connections of the Cerebellum are peculiarly unfavourable to any such influence; these being, as we have seen, rather with the lower than with the higher portion of the Cerebro-spinal axis.—Again, the results of fair observation as to the com-

have arrived at almost purely negative results in regard to the function of the Cerebellum. The former experimenter holds that this organ is not a nervous centre for sensitive impressions nor for consciousness, nor is it even a part through which the conductors of motion or of sensation pass; for he believes that no idea, emotion, or voluntary act is suppressed as a consequence of lesion of its structure. Hence he maintains, that it is not a centre for the faculty of balancing or co-ordination of the symmetrical movements of the body, and that when paralysis is observed after lesion of its structure, it is occasioned (when the paralysis is on the opposite side of the body) by concurrent lesions of other parts, as the Pons Varolii, the Medulla oblongata, or the Cerebral peduncles; whilst, when the paralysis is on the same side, it is *usually* due to *irritation* of certain parts of the Cerebellum reacting on other parts of the Encephalon, though even from this cause the paralysis may sometimes occur on the opposite side. Though he does not admit it to be a centre for auditory or visual impressions, he acknowledges that it has a special influence on vision, having collected sixty cases of amaurosis accompanying disease of its structure. (See also on this point the works of Lussana, Luys, and Renzi.) He has, in a more recent paper ("Journ. de la Phys.," 1862, tom. v. p. 486), attributed the various effects of Cerebellar lesion, as amaurosis, vomiting, cephalalgia, dilatation of the pupil, general or local convulsive movements, epilepsy, hemiplegia, general debility and disordered movements, contraction of particular muscles, strabismus, hyperæsthesia, noises in the ears, and exaggeration of the sexual desire, to *irritation* of the Cerebellum, and not to *loss of function*. He compares these effects with those produced by worms in the intestines. Wagner believes that this organ may become the *point de départ* of a direct (not reflex) irritation for certain organic muscles, as for those of the abdominal viscera, generative organs, and also, probably, for the heart. Lussana concludes the Essay already quoted, by observing that the *muscular sense* and the *erotic sense* are the two essential functions of the Cerebellum. Prideaux, "Med. Times and Gaz.," 1864, vol. ii. p. 340, adduces evidence to show that the lateral lobes are the centres of cutaneous sensibility, whilst the central lobe is the centre of muscular sensibility.

* "Med. Times and Gaz.," July 12, 1873.

parative size of the Cerebellum in different animals, can scarcely be regarded as otherwise than very unfavourable to the doctrine in question.*—It is asserted, however, that the results of observation in Man lead to the positive conclusion, that the size of the Cerebellum is a measure of the intensity of the sexual instinct in the individual. This assertion has been met by the counter-statement of others, that no such relation exists. It is unfortunate that here, as in many other instances, each party has registered the observations favourable to its own views, rather than those of an opposite character; so that until some additional evidence of a less partial nature shall have been collected, we must consider the question as *sub judice*. It may be safely affirmed, however, that no evidence upon the affirmative side of this proposition has yet been adduced, which can be in the least degree satisfactory to the mind of any Physiologist who is competent to judge of its value. For nearly all the observations which have been paraded by Phrenologists in support of Gall's doctrine, have been based, *not* upon the actual *determination* of the size or weight of the Cerebellum in different individuals, but upon an *estimate* of its proportional development from the external conformation of the skull. Now any one who has even cursorily examined those principal types of cranial conformation which are characteristic of some of the chief sub-divisions of the Human species, must perceive that there is a no less characteristic difference between these different types in the occipital than there is in the frontal region. For whilst the occipital projection is much *greater* in the 'prognathous' skull than it is in the 'elliptical,' it is as much *less* in the 'pyramidal;' and thus while the first would be considered, according to phrenological rules, to hold a much larger Cerebellum, this organ in the latter would be regarded as necessarily very small. Now there is not only as much evidence of a strong development of the sexual propensity, in the characters and habits of the pyramidal-skulled Asiatics, as there is in regard to the elliptical-skulled Europeans, or the prognathous Negroes; but there is also anatomical evidence to show that the *size of the Cerebellum in the different races bears no relation whatever to the degree of projection of the occiput;* for the plane of this organ being somewhat oblique in the elliptical skull, is horizontal in the prognathous, and nearly vertical in the pyramidal, while the size and anatomical relations of the organ are not in the least degree affected by this difference in its position.†—Hence it may be safely affirmed, that no evidence with regard to the relation asserted to exist between the size of the Cerebellum and the intensity of the sexual propensity, has any value, save that which is drawn from the positive determination of the former by measure or weight.

507. Among the arguments adduced by Gall and his followers in proof of the connection between the Cerebellum and the sexual instinct, is one which would deserve great attention, if the facts stated could be relied on. It has been asserted, over and over again, that the Cerebellum, in animals which have been castrated when young, is much smaller than in those which have retained their virility—being, in fact, *atrophied* from want of power to act. Now it is unfortunate that vague assertion, founded on estimates formed by the eye from the cranium alone, is all on which this position rests; and it will be presently shown how very liable to error such an estimate must be. The following is a result of a series of observations on this subject, suggested by M. Leuret,‡ and carried into effect by M. Lassaigne:—The *weight* of the

* See "Brit. and For. Medical Review," vol. xxii. pp. 535–541.

† The Author's statements on this point are based on the very decided assertions of his late friend Prof. Retzius of Stockholm, who paid special attention to this inquiry.

‡ "Anat. Comp. du Système Nerveux," tom. i. p. 427.

Cerebellum, both absolutely and as compared with that of the Cerebrum, was adopted as the standard of comparison. This was ascertained in ten Stallions, of the ages of from nine to seventeen years; in twelve Mares, aged from seven to sixteen years; and in twenty-one Geldings, aged from seven to seventeen years. The average weight of the Cerebrum in the *Stallions* was 433 grammes; the greatest being 485 gr., and the least (which was in a horse ten years old) being 350 gr. The average weight of the Cerebellum was 61 gr.; the greatest being 65 gr., and the least 56 gr. The average proportion borne by the weight of the Cerebellum to that of the Cerebrum, was, therefore, 1 to 7·07; the highest (resulting from the very small Cerebrum) being 1 to 6·25; and the lowest (resulting from an unusually large Cerebrum) being 1 to 7·46. Throughout it might be observed, that the variation in the size of the Cerebellum was much less than in that of the Cerebrum.—In the twelve *mares*, the average weight of Cerebrum was 402 gr.; the highest being 432 gr., and the lowest 363 gr. That of the Cerebellum was 61 gr.; the highest being 66 gr. (which was in the individual with the smallest Cerebrum), and the lowest 58 gr. The average proportion of the weight of the Cerebellum to that of the Cerebrum was 1 to 6·59; the highest being 1 to 5·09, and the lowest 1 to 7. The proportion was, therefore, considerably higher in the perfect female than in the perfect male.—In the twenty-one *Geldings*, the average weight of the Cerebrum was 419 gr.; the highest being 566 gr., and the lowest 346 gr. The average of the Cerebellum was 70 gr.; the highest being 76 gr., and the lowest 64 gr. The average proportion was, therefore, 1 to 5·97; the highest being 1 to 5·16, and the lowest 1 to 7·44. It is curious that this last was in the individual which had the largest Cerebellum of the whole; but the proportional weight of the Cerebrum was still greater.—Bringing together the results of these observations, they are found to be quite opposed to the statement of Gall. The weight of the Cerebrum, reckoning the Cerebellum as 1, is thus expressed in each of the foregoing descriptions of animals:—

	Average.		*Highest.*		*Lowest.*
Stallions	7·07	...	7·46	...	6·25
Mares	6·59	...	7·00	...	5·09
Geldings	5·97	...	7·44	...	5·16

The average *proportional* size of the Cerebellum in Geldings, therefore, is so far from being *less* than that which it bears in entire Horses and Mares, that it is positively greater; and this depends not only on diminution in the relative size of the Cerebrum, but on its own larger dimensions, as the following comparison of *absolute* weights will show:—

	Average.		*Highest.*		*Lowest.*
Stallions	61	...	65	...	56
Mares	61	...	66	...	58
Geldings	70	...	76	...	64

The difference is so remarkable, and appears, from examination of the individual results, to be so constant, that it cannot be attributed to any accidental circumstance arising out of the small number of animals thus examined. The average weight of the Cerebellum in the ten Stallions and twelve Mares is seen to be the same, and the extremes differ but little in the two; whilst the average in the Geldings is more than one-seventh higher, and the *lowest* is considerably above the *average* of the preceding, while the highest far exceeds the highest among the entire Horses. It is curious that Gall would have been much nearer the truth if he had said that the dimensions of the

Cerebrum are usually reduced by castration; for it appears from the following Table that such is really the case:—

	Average.	*Highest.*	*Lowest.*
Stallions	433	485	350
Mares	402	432	336
Geldings	419	566	346

The weight of the largest Cerebrum of the Gelding is far above the highest of the Stallions, but it seems to have been an extraordinary case, as in no other was the weight above 490 gr. If this one be excluded, the *average* will be reduced still further, being then about 412; this may be seen, by looking over the whole Table, to give a very fair idea of the usual weight in these animals, which is therefore *less*, by about one-twentieth, than the average in the Stallion.—The increased size of the Cerebellum in Geldings may perhaps be accounted for, by remembering that this class of horses is solely employed for its muscular power, and that the constant exercise of the organ is not unlikely to develop its size; while Stallions, being kept especially for the purpose of propagation, are much less applied to occupations which call forth their motor activity.

508. It is asserted, however, by the followers of Gall, that very strong evidence of the truth of this doctrine is afforded by Pathological phenomena: excitement of the genital organs, manifesting itself in priapism, turgescence of the testes, and seminal emissions, being an ordinary concomitant of some forms of apoplexy in which the Cerebellum is affected; whilst in other cases of disease or injury involving extensive destruction of the substance of the organ, there has been a complete abatement of sexual desire. The proportion of recorded cases of disease of the Cerebellum, however, in which any affection of the genital organs has been noticed, is extremely small; for out of 178 cases which have been collected by Burdach,* only 10, or scarcely more than 1 in 18, presented any symptoms that tended to indicate a functional relation between the Cerebellum and the Genital organs. The same physiologist affirms that similar affections present themselves when the Cerebrum is the seat of the lesion; and there seems a strong probability that it is solely to the connection of these organs with the Spinal cord, that such affections of the genital apparatus are due. For erection of the penis has been noticed in a far larger proportion of cases in which the Spinal cord itself has been the seat of the lesion; thus in 15 cases in which the cervical portion of the Cord was affected, erection of the penis was observed in 8; and in 13 cases of lesion of the dorso-lumbar portion of the Cord, erection of the penis took place in 3.† It is well known that erection of the penis and emissio seminis are not infrequent phenomena of death by hanging; and this fact accords fully as well with the idea that the affection of the sexual organs is consequent upon lesion of the Cranio-spinal axis, as with the doctrine that it is due to disordered functions of the Cerebellum.—It has been suggested by Serres,‡ who collected seven cases in which excitement of the genital organs was coincident with apoplexy of the median lobe of the Cerebellum, that while the lateral lobes or hemispheres may be connected with the locomotor function, the median lobe may be the organ of the sexual instinct. Several cases have been recorded in which some such relation appeared to be indicated; and the Author has been made acquainted with at least six§ in which

* "Von Bau und Leben des Gehirns" (Leipzig, 1819–26), Band iii.

† See the "Traité des Maladies de la Moëlle Epinière" of M. Ollivier (d'Angers), 3ème édit., tom. iii. p. 316.

‡ "Anatomie Comparée du Cerveau," tom. ii. pp. 601, 717.

§ Four such cases came under the notice of his friend, the late Dr. Simpson, of York.

an extraordinary salacity developed itself at an advanced period of life, whilst, concurrently with this, or following upon it, there was that kind of unsteadiness of gait which may be held to indicate chronic disease of the Cerebellum. In one of these cases of which the history and post-mortem appearances have been carefully recorded by Mr. Dunn,* there was strong evidence that the excitement of the sexual propensity was coincident with the irritative stage of incipient disease in the central lobe of the Cerebellum, and that the abatement of the propensity was in like manner coincident with the subsequent destruction of its substance; whilst the advance of the disease into the lateral lobes was marked by impairment of the power of co-ordination of movement. But with regard to all such cases, and others that may be ranked in the same category,† the objection of Pétrequin‡ holds good, that when disease or injury affects the median lobe of the Cerebellum, the Medulla oblongata is almost certain to be implicated in it; so that, as the evidence already referred to clearly indicates the existence of a special relation between the genital organs and the upper part of the Spinal axis, no positive proof is afforded by them that any portion of the Cerebellum has any special connection with the generative function.

509. The Author is far from denying *in toto* that any peculiar connection exists between the Cerebellum and the Genital system; but if the evidence at present adduced in support of the Phrenological position be held sufficient to establish it, in defiance of so many opposing considerations, we must bid adieu to all safe reasoning in Physiology. The weight of testimony appears to him to be quite decided, in regard to the connection of the Cerebellum with the regulation of the motor function; and as an additional argument in favour of this view, it may be stated, that the lobes of the Human Cerebellum undergo their most rapid development during the first few years of life, when a large number of complex voluntary movements are being learned by experience, and are being associated by means of the muscular sensations accompanying them; whilst in those animals which have, immediately after birth, the power of regulating their voluntary movements for definite objects, with the greatest precision, the Cerebellum is more fully developed at the time of birth. In both instances it is well formed and in active operation (so far as can be judged of by the amount of circulation through it), long before the sexual instinct manifests itself in any perceptible degree.—But neither doctrine need be maintained altogether to the exclusion of the other; and there are many among the Phrenologists of the present day, who hold, with Serres, that whilst the *hemispheres* of the Cerebellum possess the endowments now generally assigned to them by Physiologists, the *central lobe* is connected with the Genital function. If has been shown by Dr. N. S. Davis,§ however, that there is no perceptible difference in the dimensions of this central lobe, any more than in those of the hemispheres, between Bulls and Oxen; and no proof has yet been offered,

* "Medico-Chirurgical Transactions," vol. xxxii.

† Thus, a case has been communicated to the Author by Mr. Turley, of Worcester, in which the sexual desire, which had been always strong through life, but which had been controlled within the limits of decency, manifested itself, during a period of some months preceding death, in a most extraordinary degree; on *post-mortem* examination, a tumour was found on the Pons Varolii.—And he has been informed of another case by Dr. Evanson (formerly of Dublin), in which a young officer on the eve of marriage, having received a blow on the occiput by a fall from his horse, became impotent, without any other disorder of his bodily or mental powers; and in the distress consequent upon this discovery, committed suicide on the morning fixed for his wedding.

‡ 'Sur quelques points de la Physiologie du Cervelet et de la Moëlle Epinière,' in "Gaz. Médicale," 1836, tom. iv. p. 546.

§ "Transactions of American Medical Association," vol. iii. p. 415.

save that afforded by the pathological evidence just referred to, that any such endowment is possessed by it. That in some way or other, however, either the central portion of the Cerebellum, or some part of the Medulla oblongata, has a special connection with the Generative function, appears to the Author to be indicated with tolerable clearness by several of the Pathological phenomena already cited. The circumstance, too of which he has frequently been assured, that great application to gymnastic exercises diminishes for a time the sexual vigour, and even totally suspends desire, seems worthy of consideration in reference to such a view; for if the Cerebellum be really connected with both kinds of function, it does not seem unreasonable that the excessive employment of it upon one should diminish its energy in regard to the other. —An analysis of the nature of the Sexual propensity, however, suggests the conclusion that we are not to look in this part of the Encephalon for anything else than a seat of the sexual *sensation;* the character of which seems to be sufficiently different from that of mere *tactile* sensation, to require a distinct ganglionic centre. Such a centre would be likely to be placed in the line of the other sensory ganglia, and in close connection with them.

510. As in the case of other sensations, the Sexual, when moderately excited, may give rise to ideas, emotions, and desires, of which the Cerebrum is the seat; and these may react on the muscular system through the Intelligence and Will. But when inordinately excited, or when not kept in restraint by the Will, the sexual sensations will at once call into play respondent movements which are then to be regarded as purely automatic. This is the cause in Nymphomania and Satyriasis in the Human subject; and it is probably also the ordinary mode of operation of this sense, in such of the lower animals as have not psychical power enough to form a conception of an absent object of gratification, and cannot, therefore, be said to have sexual *desires*. Thus, like other sensations, it may act either *intelligently* or *automatically;* giving rise to *ideas*, by transmission to the Cerebrum, which ideas, associated with pleasurable feelings, originate *desires* that stimulate the Reasoning powers to devise means for their gratification, and excite the Will to the necessary actions; or, by its immediate action upon the motor-apparatus, producing respondent *movements*. —Of this double *modus operandi* we seem to have sufficient evidence. For among many of the lower tribes of animals, at the time when the generative organs are in a state of functional activity, the presence of an individual of the opposite sex indicated by the sight, smell, hearing, or touch, immediately excites the whole train of instinctive actions concerned in the reproductive operation; whilst we have no evidence in them of any voluntary exertion, resulting from the existence of a desire entertained in the absence of the object, and intended for the gratification of that desire. In Man, on the other hand, the principal operation of the sexual sensations is in awakening desires and affections, which serve as excitements to the intelligence and as motives to the Will; and it is only, under ordinary circumstances, when the two sexes have been thus brought into close relation, that the direct reaction of the sexual sensation manifests itself in automatic movements. In cases, however, in which this sensation is excited in unusual strength, it may completely overmaster all motives to the repression of the propensity, and may even entirely remove the actions from volitional control; and a state of a very similar kind exists in many Idiots, in whom the sexual propensity exerts a dominant power, not because it is in itself peculiarly strong, but because the Intelligence being undeveloped, it acts without restraint or direction from the Will.

5. *The Cerebrum, and its Functions.*

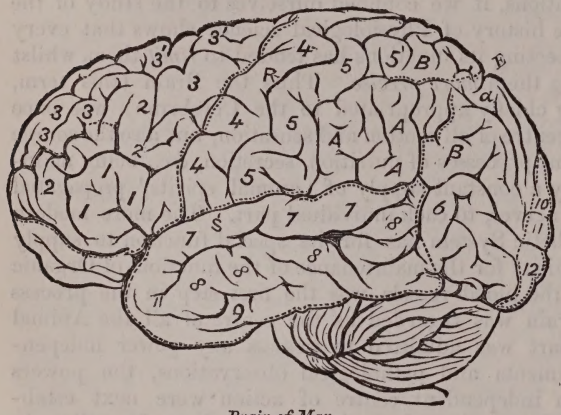
511. We come, in the last place, to consider the functions of that portion of the Nervous Centres which is evidently, in Man, the predominant organ of his whole system; being not merely the instrument of his Reasoning faculties, but also possessing a direct or indirect control over nearly all the actions of his corporeal frame, save those purely vegetative processes which are most completely isolated from his animal powers. We should be in great danger, however, of coming to an erroneous conclusion as to the real character of the Cerebrum and of its operations, if we confined ourselves to the study of the Human organism; and the history of Physiological science shows that every advance of knowledge respecting its functions has tended to *limit* them, whilst at the same time rendering them *more precise*. Thus the Brain (this term, in the old Anatomy, being chiefly appropriated to the Cerebrum) was once accounted not merely the centre of all motion and sensation, but also the source of all vitality; the different processes of nutrition, secretion, &c., being maintained, it was supposed, by a constant supply of 'animal spirits,' propagated from the brain, along the nerves, to each individual part. The more modern doctrine, that the Sympathetic System has for its special function to supply the nervous influence requisite for the maintenance of the functions of Organic life through its action on the blood-vessels, was the first step in the process of limitation; still the Brain was regarded as the centre of all the Animal functions, and no other part was admitted to possess any power independently of it. By experiments and pathological observations, the powers of the Spinal cord as an independent centre of action were next established; and it was thus shown that there is a large class of motions in which the Brain has no concern, and that the removal of the Cerebral hemispheres is not incompatible (even among the higher Vertebrata) with the prolonged maintenance of a sort of inert and scarcely conscious life. Still, it has been usually maintained, and with great show of reason, that the Cerebrum is the instrument of all *psychical* operations, and the originator of *all* the movements which could not be assigned to the reflex action of the Spinal cord. An attempt has been made, however, in the preceding pages, to show that this view is not correct; and that there is a class of actions, neither excito-motor nor voluntary, but directly consequent upon Sensations, and constituting (with the excito-motor) the truly *instinctive* actions, which may be justly assigned to certain ganglionic centres not less independent of the Cerebrum than is the Spinal cord itself. It has been further pointed out that the Cerebrum must be considered in the light of an organ *superadded* for a particular purpose or set of purposes, and not as one which is essential to life; that it has no representative among the Invertebrata (except in a few of the highest forms, which evidently present a transition towards the Vertebrate series); and that, at its first introduction in the class of Fishes, it clearly performs a subordinate part in the general actions of the Nervous System. Hence, whatever be the function, or set of functions, we assign to the Cerebrum, we must keep in view the *special* character of the organ; and we must never lose sight of the fact, that its predominance in Man does not deprive other parts of their independent powers, although it may keep the exercise of those powers in check, and may considerably modify their manifestations.

512. Before proceeding to inquire into the Physiology of the Cerebrum we may advantageously take notice of some of the leading features of its structure.*

* For further details of the minute anatomy of the Cerebral substance, see Lockhart Clarke in the "Proceedings of the Royal Society," vol. xii. No. 57. Luy's "Leçons sur la Structure du Systéme Nerveux," 1875. Hoffmann-Schwalbe, "Lehrbuch der Neurologie," 1880.

In the first place, it forms an exception to the general plan on which the elements of ganglionic centres are arranged, in having its vesicular substance on the *exterior*, instead of in the *central* part of the mass. The purpose of this is probably to allow the vesicular matter to be disposed in such a manner as to present a very large *surface*, instead of being aggregated together in a more compact mass; and by this means to admit, on the one hand, a more ready access of the blood-vessels which are so essential to the functional operations of this tissue, as well as a more ready communication, on the other, with the vast number of fibres by which its influence is to be propagated. There is no reason whatever to believe, that the relative functions of the vesicular and fibrous substances are in the least altered by this change in their relative position; indeed, the results of observation upon the phenomena of disordered Cerebral action are such as to afford decided confirmation of the doctrine now generally accepted, that the action of the Vesicular matter constitutes the *source* of nervous power, whilst the Fibrous structure has for its office to *conduct* the influence thus generated to the points at which it is to operate. The purpose of this arrangement is further evidenced by the fact, that, in all the higher forms of Cerebral structure, we find a provision for a still greater extension of the surface at which the vesicular matter and the blood-vessels may come into relation; this being effected by the plication of the layer of vesicular matter into 'convolutions,' into the sulci between which the highly vascular membrane known as the 'pia mater' dips down, sending multitudes of small vessels from its inner surface into the cortical substance. The convolutions of the Brain* are extremely complicated in their arrangement, but they can be divided into groups by certain easily recognized fissures, and are individually identified and named. The more important of them only need be described here. The outer and under surface of each hemisphere is divided into five lobes as follows. Tracing the deep Sylvian fissure outwards upon the external aspect of the hemisphere it is seen to bifurcate, one branch running upwards, the other almost horizontally backwards. Anterior to the Sylvian fissure we have the *frontal lobe*, between its two branches the *parietal lobe*, below the posterior branch the *temporo-sphenoidal lobe*, and forming the posterior extremity of the hemisphere the *occipital lobe*, while concealed within the Fissure of Sylvius is the *central lobe*, more commonly known as the Island of Reil. This last presents a few short and almost straight gyri radiating from the inner end of the fissure called the *Gyri operti*. The four other lobes are each made up of three more or less tortuous gyri. The frontal convolutions have a horizontal direction, and form three tiers, named respectively the *superior*, *middle*, and *inferior frontal* convolutions, the superior close to and parallel with the great longitudinal fissure, the inferior resting upon the orbital plate of the frontal bone. It is the posterior part of this inferior frontal convolution which has been said to be the seat of the faculty of language, and disease here to be one of the causes of aphasia. The convolutions of the parietal lobe are nearly vertical, and run up to the margin of the longitudinal fissure; between the first or anterior and the second is a well-marked sulcus, which appears early in the development of the brain, and is called the Fissure of Rolando. The temporo-sphenoidal gyri are again almost horizontal, lying parallel to the horizontal branch of the Sylvian fissure. The occipital lobe is small and not well-defined, a series of short irregular convolutions connecting it with the parietal lobe. These have received the name of annectent or bridging gyri; the

FIG. 242.



Brain of Man.

1, 2, 3, Frontal convolution. 4, 5, 6, A & B, Parietal convolutions. 7, 8, 9, Temporo-sphenoidal convolutions. 10, 11, 12, Occipital convolutions. A is the supra-marginal lobule; B is the postero-parietal lobule; and β is on the bridging or annectent convolutions; R, fissure of Rolando; E, parieto-occipital fissure.

* For accurate descriptions of which see Prof. Turner's Pamphlet, 1866; Gratiolet, "Sur les Plis Cérébraux de l'Homme," &c., 1854; L. Marshall on the 'Brain of a Bushwoman,' &c., "Proc. Roy. Soc. 1863;" Quain and Sharpey's "Anatomy," vol. ii. p. 531; and Ecker's pamphlet "On the Convolutions of the Brain."

convolutions of the occipital lobe itself are irregularly horizontal, and its anterior limit is a sulcus which issues from the longitudinal fissure, and is called the parieto-occipital fissure. On the opposed flat surfaces of the hemispheres the principal convolutions seen are the *marginal convolutions*, which form the margin of the great longitudinal fissure and the *gyrus fornicatus*, which encircles the corpus callosum, commencing anteriorly near the anterior perforated space, and terminating at the point of the temporo-sphenoidal lobe. By some anatomists these two great convolutions have been subdivided.

513. The *Cortical* substance or 'grey matter' of the Hemispheres essentially consists of that *vesicular* nerve-substance, which, in the Spinal cord, as in ganglionic masses generally, is found to occupy the interior. Its usual thickness is about one-fifth of an inch; but considerable variations present themselves in this respect, as also in the depth of the convolutions. Thus, the plications are deepest, and the layer of 'grey matter' the thickest, during the period of greatest nervous energy, that is, in middle life; in infancy and in

FIG. 243.

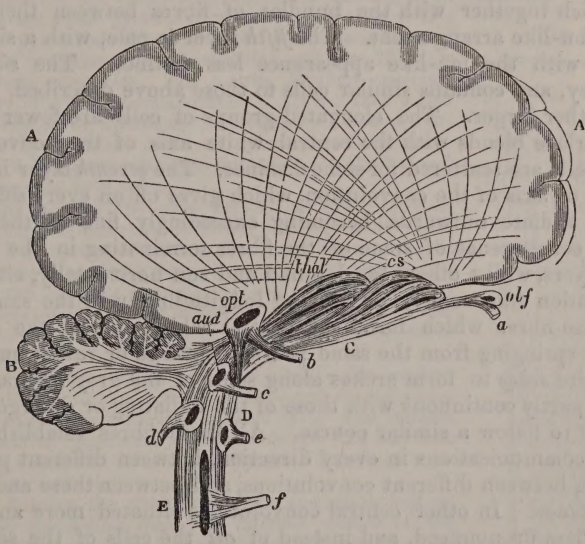


Diagram of the mutual relations of the principal Encephalic centres, as shown in a vertical section:—A, Cerebrum; B, Cerebellum; C, Sensori-motor tract, including the Olfactory ganglion *olf*, the Optic *opt*, and the Auditory *aud*, with the Thalami Optici *thal*, and the Corpora Striata *cs*; D, Medulla Oblongata; E, Spinal Cord;—*a*, olfactory nerve; *b*, optic; *c*, auditory; *d*, pneumogastric; *e*, hypoglossal; *f*, spinal: fibres of the medullary substance of the Cerebrum are shown, connecting its ganglionic surface with the Sensori-motor tract.

old age, the convolutions are simpler and have fewer undulations, and the thickness of their cortical substance is much inferior; and the same is true of the adult brain of some of the least cultivated races of mankind. The structure of the cortical substance has been most carefully investigated by Mr. Lockhart Clarke.* The convolutions present on section at least seven layers of nervous substance, the concentric arrangement of which is most conspicuous at the extremity of the posterior lobe, and is rendered apparent by a slight

* See "Proceed. of Roy. Soc.," vol. xii. No. 57, and Dr. Maudsley's "Physiology and Pathology of the Mind," 1868, p. 60, from which last the account in the text is taken. A good description of the structure of the brain is also given by Arndt in Schultze's "Archiv," Band iii. p. 441, 1867. See also Cleland, "Quart. Journ. of Microscop. Sci.," 1870, p. 126; and Meynert, in Stricker's "Human and Comp. Histology," vol. ii. p. 382; Gerlach, "Centralblatt," 1872, p. 273; Rindfleisch, "Centralblatt," 1872, p. 277; Lewis and Clarke, "Proceed. Roy. Soc.," vol. xxvii. 1878, p. 38.

difference in hue. In this situation all the nerve cells are small, but differ considerably in shape, and are much more abundant in some layers than in others. In the *superficial* layer (Fig. 244), which is pale, they are round, oval, fusiform, or angular, but not numerous. The *second* layer is darker, and is densely crowded with cells of similar form and size, mingled with others that are *pyriform* and lie with their tapering ends either towards the surface or parallel with it, in connection with fibres which run in a corresponding direction. The broader ends of the pyramidal cells give off two or more processes which run partly towards the central white axis of the convolutions, and partly horizontally along the plane of the layer. The *third* layer is of a much paler colour. It is crossed at right angles by narrow and elongated groups of small cells and nuclei, intermediate to which are bundles of fibres radiating towards the surface from the central white axis of the convolutions. The *fourth* layer contains broader and more regularly arranged groups of cells and nuclei, which together with the bundles of fibres between them, present a distinctly fan-like arrangement. The *fifth* layer is pale, with a similar structure, but with the fan-like appearance less distinct. The *sixth* layer is reddish-grey, and contains similar cells to those above described, with others that are rather larger. The elongated groups of cells are fewer in number. Its deep surface blends with the central white axis of the convolution, into which its cells are scattered for some distance. The *seventh* layer is the central white stem or axis of the convolution, which gives off on every side bundles of fibres that radiate outwards, becoming exceedingly fine as they reach the surface, in consequence of some of the fibres terminating in the cells of the different layers, whilst others bend round and run horizontally, either crossing the convolution transversely, or running longitudinally in the same direction. Besides these fibres which form the central white axis of the convolution, another set springing from the same source converge or rather curve inwards from opposite sides to form arches along some of the grey layers. They appear to be partly continuous with those of the radiating or divergent set which bend round to follow a similar course. All these fibres establish an infinite number of communications in every direction, between different parts of each convolution, between different convolutions, and between these and the central white substance. In other central convolutions situated more anteriorly, the layers are less pronounced, and instead of *all* the cells of the several layers being small, a certain proportion of much larger cells are found chiefly occupying the two internal layers. These cells are pyramidal, with quadrangular bases directed towards the central white substance, and each gives off four or more processes which run partly towards the central white axis, and partly parallel with the surface of the convolution to be continuous with arciform fibres. The processes frequently subdivide into minute branches, which form part of the network between them. The apical extremity runs straight outwards, and gives off minute branches which are lost like the process itself in the surrounding network. Slight modifications occur in the vesicular structure of other convolutions. It is interesting to note that Mr. Clarke was unable to perceive any difference whatever between the cells of the convolutions in Man and those of the ape tribe.

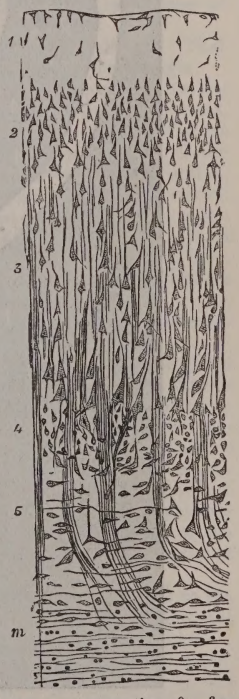
Professor Meynert, in an elaborate essay, has recently given an anatomical description of the brain, of which the following is an outline. Many points, however, are here unavoidably omitted, especially those relating to the structure of the medulla oblongata and pons, for which the reader is referred to the original article contained in the second volume of Stricker's "Manual of Histology," translated for the Sydenham Society.

Prof. Meynert points out that the peripheric nerves of the body collectively converge towards the grey matter of the cerebral cavities, spinal cord, and medulla oblongata, and that after

passing through these with more or less interruption or segmentation in the ganglion cells, they diverge to terminate in the great expansion of grey substance which forms the cortex of the cerebral hemispheres. The entire collection of fibres he terms the "Projection system," and commences its description, not with the peripheric nerves, but from the hemispheres of the cerebrum and cerebellum. He divides it into three links, with three masses of grey matter. The first mass of grey matter is the cortex of the cerebrum, and cerebellum (C, Fig. 245), and the first link of the projection system is represented essentially by the corona radiata (1, 2, 3, and 4) which consists of fibres extending from the cerebral cortex to the ganglionic masses of the corpus striatum and optic thalamus, which constitute the second mass of grey matter. The *second link* of the projection system is composed of fibres that extend from these ganglia to the grey substance around the central cavities, which is the third grey mass, and is represented by the system of the crus cerebri (5, 7, 8). The *third link* is formed by the *nerves* which arise from the above-named grey substance of the central cavities, beginning with the origin of the third pair of cerebral nerves in the grey matter around the aqueduct of Sylvius to the nucleus of origin of the lowermost coccygeal nerve of the spinal cord.

Speaking generally, the cortex of the cerebrum presents five laminæ (Fig. 244). The first is principally composed of an equably punctated matrix, with a few small stellate cells, and near its surface numerous fine varicose nerve-fibres decussating in all directions. The second is a layer of close-set, small pyramidal corpuscles; the third is a layer of large pyramidal corpuscles; the fourth is a layer of small, close-set, irregular shaped corpuscles, and the fifth is a layer of fusiform corpuscles. The matrix, Meynert considers consists chiefly of a non-nervous substance. It has been called ependyma formation by Rokitansky, neuroglia by Virchow, connective tissue by Kölliker, coalesced ganglion cell-substance by Henle and R. Wagner, gelatinous substance by Clarke, and molecular substance by Kupffer.

Fig. 244.



Transparent section of a furrow of the third central convolution of Man, × 100 diam. 1. Layer of scattered small cortical corpuscles. 2. Layer of close-set, small, pyramidal, cortical corpuscles. 3. Layer of large pyramidal corpuscles. 4. Layer of small, close-set, irregularly-shaped, cortical corpuscles (granule-like formation). 5. Layer of fusiform cortical corpuscles. *m*. Medullary layer.

The different parts of the same hemisphere are connected, first, by the numerous intercommunicating processes of the cells; and secondly, by a system of arcuate fibres of different lengths lying immediately beneath the cortex (a a, c c). The corresponding parts of the *opposite* hemispheres are connected by the transverse fibres of the corpus callosum. The cortex of the cerebrum is connected with that of the cerebellum by fibres passing directly from one to the other.

The *corpus striatum* consists of two nuclei—the caudate or intra-ventricular nucleus (Cs, Fig. 245)—and an extra-ventricular one, named the lenticular nucleus (Nl). The caudate nucleus is essentially connected with the olfactory lobe and bulb by connecting fibres, and is consequently small in man as compared with many animals.

The fibres forming the *first link of the projection system*, are—1. Those proceeding from the internal surface of the whole length of the cerebral hemisphere, but chiefly from the frontal lobes to the *lenticular nucleus*. 2. The stria cornea proceeding from the apex of the temporal lobe to the anterior region of the corpus striatum. 3. The fibres entering the *optic thalamus*—namely, *a*. Those arising from the frontal lobe and passing straight back between the caudate and lenticular nuclei of the corpus striatum (5, Fig. 245). *b*. Those proceeding from the walls of the Sylvian fissure and from the temporal lobes (inferior peduncle of optic thalamus). *c*. Fibres from the stria zonalis; and lastly, *d*. Those proceeding from the cortex of the gyrus fornicatus, constituting the ascending pillar of the fornix (or superior peduncle of optic thalamus). The fornix itself is the projection fasciculus of the cortex passing to the anterior eminence of the optic thalami.

The deeper-lying part of the *optic thalamus* receiving the corona radiata contains many cells, and constitutes the red nucleus of the tegmentum. This red nucleus is the first internode of a tract that originates in the cortex of the cerebrum in a fan-like form, and stretches to the cortex of the cerebellum. The processus a cerebello ad cerebrum is a free segment of this connecting tract between the two layers of cortical substance. Beneath the above-mentioned fan is a second more slender fan of the corona radiata, which is applied to the substance of Soemmerring. Posteriorly the optic thalami are connected with the

optic tracts. The optic tracts are also connected just as if they were a portion of the corona radiata with the brachium of the inferior corpus quadrigeminum. The optic tracts and nerves, therefore, are not peripheric nerves, but the retina, like the olfactory bulb, is, so to speak, an outlying portion of the cortex cerebri.

Fig. 245.

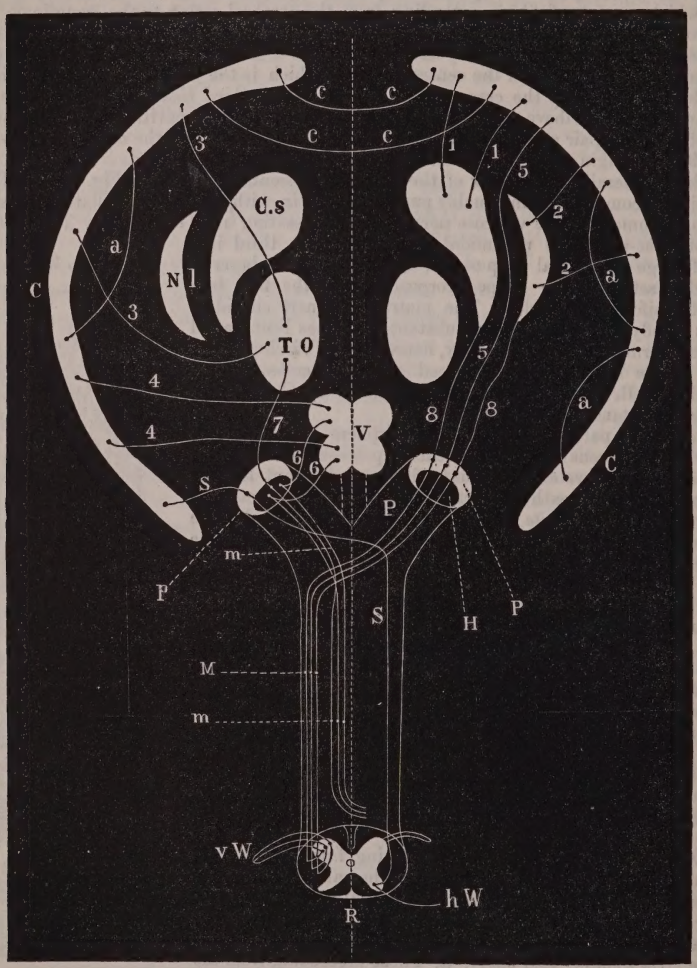


Diagram of the structure of the brain. C C, cortical substance of the cerebral hemispheres; C. s, corpus striatum; N. l, nucleus lenticularis; T. O, thalamus opticus; V, corpora quadrigemina; P, pedunculus cerebri; P, basis or crusta, and H, tegmentum; 1, 1, fibres of the corona radiata of the corpus striatum; 2, 2, those of the lenticular nucleus; 3, those of the optic thalamus; 4, 4, those of the corpora quadrigemina; 5, 5, direct strands to the cortex cerebri (Flechsig); 6, fibres from the corpora quadrigemina to the tegmentum; 7, fibres from the optic thalamus to the tegmentum; *m*, further course of these fibres; 8, fibres from the corpus striatum and lenticular nucleus to the pes of the pedunculus cerebri; M, further course of these fibres; S, S, course of the sensory fibres; R, transverse section of the spinal cord; v W, anterior roots; h W, posterior roots of the spinal nerves; a, a, association fibres; c, c, commissural fibres.

The second link of the projection system is formed by the system of the crura cerebri, which is divided into two layers with some intermediate grey substance. The inferior or anterior layer named the *crusta*, proceeds from the corpus striatum; the superior or posterior layer named the *tegmentum*, chiefly from the optic thalamus. In addition to the fibres proceed-

ing from the two nuclei of the corpus striatum, the crusta contains others derived from the substantia nigra of the ventricles and fibres which come directly from the occipital and temporal lobes. The size of the cerebral hemispheres, of the lenticular nucleus, and of the crusta cerebri, are all proportionate to one another, but there is no relation between the size of the crusta and of the tegmentum. On the contrary, the tegmentum of the crus with its ganglia, especially the corpora quadrigemina, and corpora geniculata interna, are more largely developed in proportion to the smallness of the cerebral lobes. The tegmental fibres proceeding from the optic thalamus are reinforced by others from the posterior commissure—the anterior and posterior corpus geniculatum, the cortex cerebelli, and the pineal gland, those from the latter source decussating with those of the opposite side. The innermost fibres of the crusta, after decussating in the middle line, terminate peripherally in the central grey substance of the ventricle surrounding the aqueductus Sylvii in the nates, penetrating at this point into the nucleus common to the third and fourth nerves. The most external fasciculus of the crusta passes through the decussation of the pyramids of the medulla oblongata, into the posterior column of the spinal cord.

The tegmentum is characterized by its connection with the optic tracts and fifth pair of nerves on the one hand, and with the motor columns of the spinal cord on the other, forming a region where sensory impressions are reflected as motor impulses. The fact that the ganglia of the crusta have no connection with sensorial peripheric expansions, suggests that they owe their power of exciting motor impulses to another source—namely, to the conditions of excitation of the cerebral lobes.

The organization of the crusta is completed near the anterior part of the thalamus. That of the tegmentum just below the corpora quadrigemina, the lowest of its ganglia of origin.

A large group of the radiating fibres proceeding from the occipital lobes converge to the ganglia of origin of the tractus opticus—*i.e.*, the external and internal corpora geniculata, and the corpora quadrigemina, forming a remarkably thick medullary lamina (optic radiations of Gratiolet). This mass associates itself with the posterior and *external* fasciculi of the *crusta* of the crus cerebri. But the most *external* fasciculus of the crusta, as just stated, passes through the decussation of the pyramids of the medulla oblongata, into the *posterior column* of the spinal cord, and consequently the posterior roots of the spinal nerves are represented in the same lobes of the hemispheres as the radiations of the optic tract. It is remarkable that these lobes also receive the fibres proceeding from the olfactory bulb and lobe. Another group of fibres from the cortex pass to the corpora quadrigemina, forming the brachia of the nates and testes.

The pineal gland is a ganglion of origin of the tegmentum, and is placed over the decussation of the tegmenta of the opposite sides.

At the level of the pons is a large and important region where the brachia of the cerebellum interlace with the projection system, and from this point the third link of the projection system descends. The superior peduncle is composed partly of fibres of the corona radiata, proceeding directly from the cortex of the cerebral hemispheres, and partly of the fibres from the optic thalamus and corpus striatum, all of which decussate so that the superior peduncles form a horseshoe closed in front which corresponds with the nates and testes. They constitute the *connecting* system of the cerebellum. The middle peduncle of the cerebellum is best understood by remembering that every fasciculus of the crusta terminating in the anterior division of the pons is represented by two fasciculi of the opposite middle peduncle of the cerebellum, of which one runs through the superficial, the other through the deep layer of transverse fibres of the pons.

The inferior peduncle of the cerebellum consists of fibres passing from the cerebellum to the posterior columns of the spinal cord, and includes—1. The corpus restiforme; 2. The internal division of the inferior crus cerebri, and 3. The fasciculus cuneatus and slender fasciculus.

The grey substance of the central cavities is a centre from which a large number of nerve-roots take origin. It lines the third ventricle, surrounds the aqueduct of Sylvius, expands itself in the cavity of the fourth ventricle, and encloses the central canal throughout the spinal cord; from it the third, fourth, and succeeding cerebral, and all the spinal nerves in succession take origin, and these constitute the third link of the projection system. The third nerve may in fact be taken as the type of the projection system of Meynert. The first link consists of fibres extending from the cerebrum to the lenticular nucleus; the second link from the lenticular nucleus to the nucleus of origin of the third nerve in the grey substance of the third ventricle of the opposite side, and the third link being the nerve itself.

The cerebellum represents a loop or sling, the curves and sinuosities of which establish very indirect connections between the cerebrum and the nerve-roots. The auditory nerve is almost entirely lost in it, and it has extensive connections with the optic nerve. The crusta of the cerebral peduncle, which descending, is continued into the pyramids of the medulla oblongata, is at least three times the size of the pyramids, and this diminution is due to the termination of many of the fibres of the crusta in the ganglion cells of the pons, from whence fibres arise

that pass into the middle peduncles of the cerebellum. A motor function must therefore be attributed to the cerebellum, even from this point of view alone. For no other view can be taken than that the impulses conducted from the cortex to the corpus striatum and the lenticular nucleus, besides their conduction into the spinal cord, at the same time give rise to definite modes of activity of the cerebellum.

The medulla oblongata consists of a prolongation of the anterior and posterior tracts of the crus cerebri, and of the crus cerebelli, together with much scattered grey matter in its substance, and a layer on its surface, the grey matter of the fourth ventricle representing the grey matter of the central cavities.

514. The weight of the entire Encephalon in the adult Male usually ranges between 40 and 68 oz., the average being about 50 oz.; and in the Female from 36 to 50 oz., the average being about 45 oz.* The maximum of the healthy brain seems to be about 64 oz., and the minimum about 31 oz. But in cases of Idiocy, the amount is sometimes much below this; as low a weight as 20 oz. having been recorded.—It appears, from the investigations of M. Bourgery, that the relative sizes of the different component elements of the Human Encephalon are somewhat as follows:—Dividing the whole into 204 parts, the weight of the Cerebrum will be represented by about 170 of those parts; that of the Cerebellum by 21, and that of the Medulla oblongata with the Optic thalami and Corpora striata by 13. The weight of the Spinal cord would be, on the same scale, 7 parts. Hence the Cerebral hemispheres of Man include an amount of nervous matter which is *four* times that of all the rest of the Cranio-spinal mass, more than *eight* times that of the Cerebellum, *thirteen* times that of the Medulla oblongata, &c., and *twenty-four* times that of the Spinal cord.—The absolute weight of the cerebral hemispheres varies according to Meynert from 17,000 to 21,600 grains. The average weight of the whole Encephalon in proportion to that of the body, in Man, taking the average of a great number of observations, is about 1 to 36. This is a much larger proportion than that which obtains in most other animals; thus the average of Mammalia is stated by M. Leuret to be 1 to 186, that of Birds 1 to 212, that of Reptiles 1 to 1321, and that of Fishes 1 to 5668.† It is interesting to remark, in reference to these estimates, that the Encephalic prolongation of the Medulla oblongata in Man (being about one-sixteenth of the weight of the whole Encephalon) is *alone* more than twice as heavy in proportion to his body as the *entire* Encephalon of Reptiles, and ten times as heavy as that of Fish.—But there are some animals in which the weight of the Encephalon bears a higher proportion to that of the body than it does in Man; thus in the Blue-headed Tit, the proportion is as 1 to 12, in the Goldfinch as 1 to 24, and in the Field-mouse as 1 to 31. It does not hence follow, however, that the *Cerebrum* is larger in proportion; in fact, it is probably not nearly so large; for in Birds and Rodent Mammals, the Sensory ganglia form a very considerable proportion of the entire Encephalon. M. Baillarger has shown that the *surface* and the *bulk* of the cerebral hemispheres are so far from bearing any constant proportion to each other in different animals, that notwithstanding the depth of the convolutions in the Human Cerebrum, its bulk is $2\frac{1}{2}$ times as great in proportion to its surface as it is in

* The average of both sexes differs, however, in the various races of mankind. Dr. Davis ("Proceedings of the Royal Society," Jan. 23rd, 1868) found the mean of the European series to be 46·87 oz.; of the Asiatic series, 44·62 oz.; of the American series, 44·73 oz.; of the African series, 44·3 oz.; and of the Australian series, 41·38 oz. Dr. Thurnam ("Journal of Mental Science," April, 1866) gives 49 oz. as the average weight of the European brain, whilst in distinguished men it amounts to 54·6 oz.

† In the pike the proportion is as 1 to 1300; in the horse 1 to 800; elephant 1 to 500; sheep 1 to 350; dog 1 to 110; pigeon 1 to 104. See Munk, "Archiv f. wiss. u. prakt. Thierheilkunde," Band vi. 1880, p. 73. For the influence of stature on the weight of the encephalon in man, see Marshall, "Proceed. Roy. Soc.," June 17, 1875.

the Rabbit, the surface of whose Cerebrum is smooth. The entire surface of the human Cerebrum is estimated by him at about 670 square inches. In all estimates of the weight of the Brain in Man, it is important to take the influence of stature into consideration. Professor Marshall has shown that an increase of stature is accompanied by an increase in the absolute but not in the relative weight of the brain. Taking both sexes together, the total increase, with a mean range of 11 inches between the highest and the lowest group of individuals examined, is about $6\frac{3}{4}$ oz. avoirdupois (=191·25 grammes); in males, with a mean range of 7 inches, it is $2\frac{3}{4}$ oz.; in females, with a range of 6 inches, it is $1\frac{1}{4}$ oz.; the Cerebrum in both increasing absolutely more than the Cerebellum. Further investigation, however, showed to him that this increase does not take place *pari passu* with the stature, but that, on the contrary, there is a gradual and progressive relative diminution in the proportion of Encephalic substance to the stature as this latter itself increases. Hence short persons of either sex have, proportionally to their height, a larger amount of brains than taller ones. Nevertheless, the proportion is larger in the male than in the female, not only generally but even at corresponding heights—as for example in short men as compared with tall women. This, as Mr. Marshall observes, is interesting, as evidence that the well-known sexual difference in the weight of the male brain overrides the influence of stature, or subsists in spite of his greater stature, which has a tendency to diminish his proportionate amount of brain. The specific gravity of the Brain has been made the subject of careful research by Dr. Bastian, who finds the average of the grey substance to be 1·030 and of the white 1·040.

515. The Encephalon altogether receives a supply of Blood, the amount of which is very remarkable, when its comparative bulk is considered; the proportion which goes to it being, according to the estimate of Haller, as much as one-fifth of the whole mass. The manner in which this blood is conveyed to the brain, and the conditions of its distribution, offer some peculiarities worthy of notice. The two Vertebral and two Carotid arteries, by which the blood enters the cavity of the cranium, have a more free communication by anastomosis than any similar set of arteries elsewhere; and this is obviously destined to prevent an obstruction in one trunk from interrupting the supply of blood to the parts through which its branches are chiefly distributed—the cessation of the circulation through the nervous matter being immediately productive of suspension of its functional activity.*—Not only must there be a sufficient supply of blood, but it must make a regulated pressure on the walls of the vessels. Now the Encephalon is differently circumstanced from other vascular organs, it being enclosed within an unyielding bony case; and we find a special provision for equalizing the bulk of the contents of this cavity, and for counterbalancing the results of differences in the functional activity of the brain and in its supply of blood, in the existence of a fluid which is found beneath the arachnoid, both on the surface of the brain and spinal cord, and in the ventricles of the former. The amount of this 'cerebro-spinal-fluid'† seems to average about two ounces; but in cases of atrophy of the brain, as much as twelve ounces of fluid may sometimes be obtained from the cranio-spinal cavity; whilst in all instances in which the bulk of the brain has undergone an

* M. Robin ("Journal de la Physiologie," vol. ii. p. 537) has described an accessory tissue around the capillaries of the brain, in the space between which and the proper tunica adventitia, free nuclei, fatty masses, and granules of hæmatosin, are observable. M. Robin seems to be of opinion that these are the lymphatics of the brain. See also Stricker in idem, 1867, p. 652.

† For a full discussion of the value and uses of the cerebro-spinal fluid see Hilton, "Rest and Pain," ed. Jacobson, 2nd ed., 1877, sects. ii. and iii.

increase, whether from the production of additional nervous tissue, or from undue turgescence of the vessels, there is either a diminution or a total absence of this fluid. It appears from the experiments of Magendie (to whom our knowledge of its importance is chiefly due), that its withdrawal in living animals causes great disturbance of the cerebral functions, probably by allowing undue distension of the blood-vessels; it is, however, capable of being very rapidly regenerated, and its reproduction restores the nervous centres to their natural state.—As the cerebro-spinal fluid can readily find its way from the sub-arachnoid spaces of the *cranial* cavity into those of the *spinal*, and as it is no less readily absorbed than reproduced, it evidently serves as an equalizer of the amount of pressure within the cranial cavity; admitting the distension or contraction of the vessels to take place, within certain limits, without any considerable change in the degree of compression to which the nervous matter is subjected. That this uniformity is of the greatest importance to the functional exercise of the brain, is evident from a few well-known facts. If an aperture be made in the skull, and the protruding portion of the brain be subjected to pressure, the immediate suspension of the activity of the whole organ is the result; in this manner, a state resembling profound sleep can be induced in a moment, the normal activity being renewed *as* momentarily so soon as the pressure is withdrawn.* This phenomenon has often been observed in the Human subject in cases in which a portion of the cranial envelope has been lost by disease or injury. The various symptoms of cerebral disturbance which are due to a state of general Plethora, are evidently owing to an *excess* of pressure within the vessels; but an undue *diminution* of pressure is no less injurious, as appears from the disturbance in the cerebral functions which results from the very opposite cause—namely, a depression of the power of the heart, or a deficiency of blood in the vessels.—It is of peculiar importance to bear in mind the disturbance of the cerebral functions occasioned by variations of internal *pressure*, when we are endeavouring to draw inferences from the phenomena presented by disease.

516. We shall now proceed with our Physiological inquiry into the functions of the Cerebrum; and shall appeal, as before, to Human and Comparative Anatomy, to Experiment and to Pathology, for our chief data.—The anatomical relations of the Cerebrum to the other Encephalic centres, clearly demonstrate that it is not one of the essential or fundamental portions of the Nervous system; but a superadded organ, receiving all its impulses to action from the parts below, and operating upon the body at large through them. And its great bulk, joined to its position at the summit of the whole apparatus—the vesicular substance of its convolutions affording a termination to the fibres in connection with it, and not being for the most part only traversed by them, as is the case with that of all the lower centres—clearly mark it out as the highest in its functional relations, and as ministering, so far as any material instrument may do, to the exercise of those psychical powers, which, in Man, exhibit so remarkable a predominance over the mere animal instincts. This conclusion is fully borne out, when we extend our inquiries from Human to Comparative Anatomy; for with some apparent exceptions which there would probably be no great difficulty in explaining if we were in possession of all the requisite data, there is a very close correspondence between the relative development of the *Cerebrum* in the several tribes of Vertebrata,† and the degree of *Intelligence* they respectively possess—using

* Schiff states that the Indian snake-charmers are accustomed to produce rigidity of the body in these animals by pressure on the occiput.

† See "Princ. of Comp. Phys.," § 662 *et seq.* For numerous instances of "Intellect in Brutes," see "Nature," 1879.

the latter term as a comprehensive expression of that series of mental actions which consists in the *intentional* adaptation of means to ends, based on definite *ideas* as to the nature of both. It is not always easy to say, in the case of the lower animals, what parts of their actions are to be attributed to automatic impulse (*i.e.*, to be considered as Instinctive), and what should be regarded as the results of Intelligence. The character of Intelligent actions, however, as compared with Instinctive, is usually shown (1) in the *variety* of means which are adopted to compass the same ends, and this not merely by different individuals and by successive generations, but by the same individual at different times; (2) by the improvement in the mode of accomplishing the object, which results from the intelligent use of experience, and from the greater command of means which is progressively attained; and (3) by the conformity of the means to altered circumstances, so that the character of adaptiveness is still maintained, however widely the new conditions may depart from those which must be considered as natural to the species.

517. The difference between actions which proceed from the Intellectual faculties prompted by the instinctive propensities, and those of a purely Instinctive character, is well seen in comparing Birds with Insects. The Instinctive tendencies of the two classes are of nearly the same kind; and the usual arts which both exhibit in the construction of their habitations, in procuring their food, and in escaping from danger, must be regarded as intuitive, on account of the uniformity with which they are practised by different individuals of the same species, and the perfection with which they are exercised on the very first occasion. But in the adaptation of their operations to peculiar circumstances, Birds display a variety and fertility of resource, far surpassing that which is manifested by Insects; and it can scarcely be doubted by those who attentively observe their habits, that in such adaptations they are often guided by real intelligence. This must be the case, for example, when they make trial of several means, and select that one which best answers that purpose; or when they make an obvious improvement from year to year in the comforts of their dwelling; or when they are influenced in the choice of a situation by peculiar circumstances, which in a state of Nature can scarcely be supposed to effect them. The complete domesticability of many Birds is in itself a proof of their possessing a certain degree of intelligence; but this alone does not indicate the possession of more than a very low amount of it; since many of the most domesticable animals are of the humblest intellectual capacity, and seem to become attached to Man, principally as the source on which they depend for the supply of their animal wants. But there are certain tribes of Birds, especially the Parrots and their allies, which possess an extraordinary degree of *educability*, and which manifest a power of performing simple acts of *reasoning*, that are quite comparable with those of a child when first learning to talk.

518. This development of the Intelligence under the influence of Man, and in accordance with *his* habits rather than with the original habits of their species, is yet more remarkable in the case of those Mammals whose instincts lead them to attach themselves peculiarly to him, and whose powers of reasoning are called forth in adapting themselves to the new circumstances in which they are thus placed. The actions of a Dog, a Horse, or an Elephant are evidently the result, in many instances, of a complex train of reasoning, differing in no essential respect from that which Man would perform in similar circumstances; so that the epithet 'half-reasoning,' commonly applied to these animals, does not express the whole truth; for their mental processes are of the same *kind* with those of Man, and differ more in the *degree* of compre-

hensiveness of their data and conclusiveness of their inferences, than they do in their essential character. More evidence, however, than we at present possess is required to show that any of the lower animals have a voluntary power of *directing* their mental operations, at all similar to that which Man possesses; these operations, indeed, seem to be of very much the same character as those which we perform in connected dreams, different trains of thought commencing as they are suggested, and proceeding according to the usual law, until some other disturb them.—Although it is customary to regard the Dog and the Elephant as the most intelligent among the lower animals, it is not certain that we do so with justice; for it is very possible that we are misled by that peculiar attachment to Man, which in them must be termed an instinct, and which enters as a motive into a large proportion of their actions; and that, if we were better acquainted with the physical characters of the higher Quadrumana, we should find in *them* a greater degree of mental capability than we now attribute to them. One thing is certain, that the higher the degree of Intelligence which we find characteristic of a particular race, the greater is the degree of variation which we meet with with in the characters of individuals; thus everybody knows that there are stupid Dogs, and clever Dogs, ill-tempered Dogs, and good-tempered Dogs—as there are stupid Men and clever Men, ill-tempered Men and good-tempered Men. But no one could distinguish between a stupid Bee and a clever Bee, or between a good-tempered Wasp and an ill-tempered Wasp, simply because all *their* actions are prompted by an unvarying Instinct.

519. In estimating the relative development of the Cerebrum in different tribes of Animals, and in comparing this with their relative Intelligence, it must be borne in mind that the *size* of the organ does not, considered alone, afford a means of accurate judgment as to its *power*. For the quantity of vesicular matter which it contains, affords the only fair criterion of the latter; and of this we must judge, not merely by the superficial area, but by the number and depth of the convolutions, and by the thickness of the cortical layer.* Again, there are many reasons why it is not fair to estimate the relative development of the Cerebrum by the proportion which it bears to the whole bulk of the animal; and, on the whole, the most accurate basis of comparison would probably be afforded by the relation between the bulk of the Cerebrum and the diameter of the Spinal cord. In making any such comparison, however, the Thalami optici, Corpora striata, and Corpora quadrigemina should be excluded from the estimate, for reasons now sufficiently apparent; and the bulk of the Cerebrum *proper* should be alone determined, either by weight, or by the displacement of liquid.—But the Cerebrum varies in different classes and orders of Vertebrata, not merely in proportional size, but also in the relative development of its anterior, middle, and posterior lobes. This is a point of very great importance, in determining the value to be assigned to the organological system of Gall and Spurzheim and their followers. The Cerebrum of the Oviparous Vertebrata is *not* a miniature representative of that of Man, as a whole, but only of his *anterior* lobes; as is sufficiently obvious from an examination of its connections with other parts, and from the absence of any other commissural connections between its two hemispheres than those which are afforded by the Sensory ganglia. It is in the Non-placental Mammals that we find the first rudiments of the *middle* lobes of the Cerebrum, and of the proper inter-cerebral commissure, the Corpus callosum; and even in the Rodents this is but very imperfectly

* See for numerous observations bearing on this point, Bevan Lewis, "Brain," 1878, vol. i. p. 79, and Danilewsky, "Centralblatt f. d. Med. Wiss.," 1880, p. 241.

developed. As we ascend the Mammalian series, we find the Cerebrum becoming more and more elongated posteriorly by the development of the middle lobes, and the inter-cerebral commissure becomes more complete; but we must ascend as high as the Carnivora, before we find the least vestige of the *posterior* lobes; and the rudiment which these possess is so rapidly enlarged in the Quadrumana, that in some of that group the posterior lobes are as fully developed in reference to the Cerebrum as a whole, and as completely cover in the Cerebellum as in the Human subject.*—The attention which has yet been given to this department of inquiry, has not hitherto done more than confirm the statement already made, with regard to the general correspondence between the development of the Cerebrum and the manifestations of Intelligence; very decided evidence of which is furnished by the great enlargement of the Cerebrum, and the corresponding alteration in the form of the Cranium, which present themselves in those races of Dogs most distinguished for their educability, when compared with those whose condition approximates most closely to what was probably their original state of wildness.

520. This general inference, drawn from Comparative Anatomy, is borne out by observation of the Human species. When the Cerebrum is fully developed, it offers innumerable diversities of form and size among various individuals; and there are as many diversities of character. It may be doubted if two individuals were ever exactly alike in this respect. That a Cerebrum which is greatly under the average size is incapable of performing its proper functions, and that the possessor of it must necessarily be more or less idiotic, there can be no reasonable doubt. On the other hand, that a large well-developed Cerebrum is found to exist in persons who have made themselves conspicuous in the world in virtue of their intellectual achievements, may be stated as a proposition of equal generality. In these opposite cases we witness most distinctly the antagonism between the Instinctive and Voluntary powers. Those unfortunate beings in whom the Cerebrum is but little developed, are guided almost solely by their instinctive tendencies, which frequently manifest themselves with a degree of strength that would not have been supposed to exist; and occasionally new instincts present themselves, of which the Human being is ordinarily regarded as destitute.† On the other hand, those who have obtained most influence over the *understandings* of others, have always been large-brained persons, of strong intellectual and volitional powers, whose emotional tendencies have been subordinated to the reason and will, and who have devoted their whole energy to the particular objects of their pursuit.—It is very different, however, with those who are actuated by what is ordinarily

* It has been asserted by the followers of Gall, that the development of the Cerebrum from behind forwards, as above described, is rather apparent than real: the whole organ being in fact pushed backwards by the excessive development of the anterior lobe. But the anatomical distinction between the anterior and middle lobes is sufficiently obvious externally; and that of the middle and posterior lobes is also clearly marked out by the development of the posterior cornua of the lateral ventricles, and the situation of the hippocampus major. Hence the facts above stated do not admit of any such interpretation; and they are fully borne-out by the history of the Embryonic development of the Cerebrum in Man, which precisely follows the above plan.—It is not here denied that the anterior lobe of the Human Cerebrum is remarkable for its great extension *forwards;* but still, the difference between the Cerebrum of Man and that of the lower Mammalia consists much rather in the proportional development of the posterior lobes, than in that of the anterior.

† A remarkable instance of this was published some years since:—A perfectly idiotic girl, in Paris, having been seduced by some miscreant, was delivered of a child without assistance and it was found that she had *gnawed* the umbilical cord in two, in the same manner as is practised by the lower animals. It is scarcely to be supposed that she had any idea of the *object* of this separation.

termed *genius;* and whose influence is rather upon the *feelings* and *intuitions*, than upon the understandings of others. Such persons are often very deficient in the power of even comprehending the ordinary affairs of life; and still more commonly they show an extreme want of judgment in the management of them, being under the immediate influence of their passions and emotions, which they do not sufficiently endeavour to control by their intelligent will. The life of a 'genius,' whether his bent be towards poetry, music, painting, or pursuits of a more material character, is seldom one which can be held up for imitation. In such persons, the *general* power of the mind being low, the Cerebrum is not usually found of any great size.—The *mere* comparative size of the Cerebrum, however, affords no accurate measure of the amount of mental power; for we not unfrequently meet with men possessing large and well-formed heads, whose physical capability is not greater than that of others, the dimensions of whose crania have the same general proportion, but are of much less absolute size. Large brains, with deficient activity, are commonly found in persons of what has been termed the *phlegmatic* temperament, in whom the general processes of life seem in a torpid and indolent state; whilst small brains and great activity betoken what are known as the *sanguine* and *nervous* temperaments.

521. Having now inquired into the evidence of the *general* functions of the Cerebrum, which may be derived from the examination of its comparative development, we proceed to our other sources of information, Experiment and Pathological phenomena. The electric excitability of the hemispheres was first experimentally demonstrated by Fritsch and Hitzig,* who found that on the application of a constant current to particular regions of the surface of the hemisphere exposed by removal of the bone and *dura mater*, definite muscular movements occurred on the opposite side of the body, such as flexion, extension, and rotation of the limbs, and also movement of the facial muscles. Their earlier experiments were made on dogs, and the constant currents applied were feeble. They adduced various reasons against the supposition that the movements were due to mere conduction of the stimulus to distant centres, amongst the more important of which were the feebleness of the currents employed, the close approximation of the electrodes, the bad conductivity of the brain substance, the occurrence of contractions on the opposite side of the body, and their non-appearance when the position of the electrodes was slightly altered. In further researches, Hitzig† believed he was able to establish the existence of a distinct centre for the several movements of the eyes, coinciding with a part of the Facialis centre, and especially that part innervating the protective muscles of the eye, and he concluded from his experiments on monkeys that the anterior cerebral convolution constitutes the true motor part of the cortex of the cerebrum, the several centres lying in it from the median fissure downwards to the Sylvian fissure. The centre for the posterior extremity of the opposite side was about 3 mm. from the median line, and that for the anterior extremity about 3 mm. further outwards. Seven mm. beyond this laterally he placed the centre for a part of the muscles associated with the visual organs, and close to the Sylvian fossa he recognised a fourth centre governing the muscles of the mouth, tongue, and jaw of *both* sides. Weak currents applied to the parietal and frontal regions were not followed by any movements. He subsequently‡ found that lesion of the posterior convolutions (occipital) of the cerebral hemispheres produces blindness of the opposite eye and paralytic dilatation of the corresponding pupil. Soon after the appearance of the first

* Reichert's "Archiv," 1870, p. 300.
† Ibid., 1873, p. 397; and "Berliner Klin. Wochenschr.," 1874, No. 6.
‡ "Centralblatt f. d. Med. Wiss.," 1874, p. 548.

series of observations made by Fritsch and Hitzig, the results they obtained were confirmed and extended by Ferrier.* He defined on the surface of the brain of cats, dogs, and rabbits, the different centres from which various movements of the limbs, face, mouth and tongue, eyes, ears, &c., could be definitely and distinctly excited. The method of stimulation he employed was the direct application to the surface of the hemispheres of a pair of the blunted electrodes of the secondary spiral of Du Bois-Reymond's induction coil, connected with a cell of the mean electro-motor power of a single Daniell. The induced current generated in the secondary coil at eight centimeters distance from the primary coil was of a strength sufficient to cause a pungent but quite bearable sensation when the electrodes were placed on the tip of the tongue. Other observers have shown that similar effects can be produced by the employment of chemical stimuli. From the results of his experiments on monkeys, Ferrier† mapped out the following regions in their brain, the stimulation of which gives results which may thus be briefly stated (see Figs. 246, 247):—1. Movement of the hind foot as in walking; 2. Complex movements of the hind leg, con-

Fig. 246.

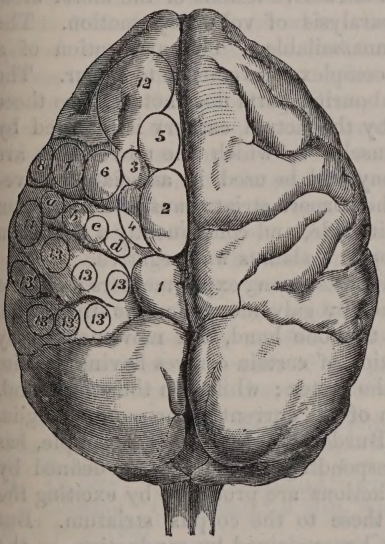
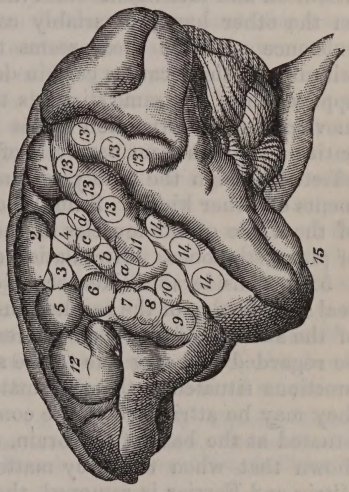


Fig. 247.


13
13
13

12. Eyes directed to the opposite side and upwards, with usually contraction of the pupils; 13. Similar action, but the eyes usually directed downwards; 14. Retraction of the opposite ear, head turning to the opposite side, the eyes widely opened and the pupils dilated; 15. Stimulation of this region, which corresponds to the tip of the uncinate convolution, causes torsion of the lip and nostril of the same side. The antero-frontal and occipital regions give no result on stimulation; nor does the island of Reil react to the stimulus. Thus it would appear that the *motor area* in monkeys includes the bases of the three frontal convolutions, with those bounding the fissure of Rolando—viz., the *ascending frontal* or anterior central (Ecker), the *ascending parietal* or posterior central (Ecker), and its upper continuation termed the *postero-parietal* or superior parietal lobule; together with the minor aspect of the same, usually named by the French the paracentral lobule. Ferrier* finds that removal or destruction by the cautery of the antero-frontal lobes is not followed by any definite physiological results. Monkeys thus operated on preserved their sensory faculties and powers of voluntary motion unimpaired, yet though not actually deprived of intelligence, they lost to all appearance the faculty of attention and intelligent observation. Destructive lesions of the motor area, on the other hand, invariably caused paralysis of voluntary motion. The existence of these areas seems to be unassailable. The application of a stimulus to them causes certain definite complex movements to occur. The application of the same stimulus to neighbouring parts does not produce those movements. Destruction of the areas by the actual cautery is followed by entire and permanent paralysis of the muscles by which the movements are effected, though the paralysed muscles may still be used in associated movements of other kinds. Stimulation of the corpora striata caused tonic spasm of the whole of the muscles of the opposite side, and consequently a condition of pleurosthotonos. Stimulation of the optic thalamus was negative.

522. Considerable difference of opinion exists among experimenters as to the real signification of the results thus obtained by galvanic or Faradic stimulation of the surface of the hemispheres. On the one hand, the movements may be regarded as being due to the stimulation of certain centres having definite functions situated in the grey matter of the cortex; whilst, on the other hand, they may be attributed to the conduction of the current to the motor ganglia, situated at the base of the brain. Dr. Burdon Sanderson,† for example, has shown that when the grey matter corresponding to the centres defined by Hitzig and Ferrier is removed, the same actions are produced by exciting the medullary fibres which proceed from these to the corpus striatum. But Ferrier‡ argues that the results cannot be explained by conduction, on the ground that in a state of anæsthesia sufficient to prevent any manifestation on stimulation of the surface of the brain, the corpora striata still remain excitable; whereas, unless it be assumed that chloroform annihilates the conductivity of the medullary fibres to the electric stimulus, the results should be obtained as before. The definiteness and predictibility of the results, the possibility of differentiating centres in close proximity to each other, and also the fact that stimulation of the island of Reil, which is near the corpus striatum, causes no action, even when the rest of the brain is excitable, seem to dispose of objections on the ground of conduction or diffusion. Ferrier further argues that as the corpus striatum contains in an integrated form the centres individually differentiated in the hemispheres, it is quite in accordance with the

* "The Localisation of Cerebral Disease," 1878, p. 36.
† "Proceed. Roy. Soc.," 1873, June 11, 1874.
‡ "West Riding Asylum Reports," vol. iv. 1874.

explanation given by Hitzig and himself to suppose that stimulation of the medullary cone of fibres should excite the same movements as result from functional activity of the corresponding cortical centres. Many experimenters,* have noticed that the excitability of the fibres of the corona radiata is completely lost on the fourth day after the section, just as in the case of the peripheral segment of ordinary nerves separated from their centre. That the movements observed on the application of an electrical stimulus are not due to any mechanical irritation or shock is evident from the fact that chemical stimuli produce the same effect as the electrical current. Landois and others have† observed that stimulation of the cortical motor centres is inoperative in recently-born animals. The first movements that could be produced in puppies were in the fore-leg, and occurred on the tenth day. Stimulation of the corpus striatum was also without effect; yet stimulation of the *capsula interna*, or deep fibres of the zona radiata, produced movements of the opposite fore-leg even in the newly-born animal. The cortical areas are of wider extent at first than at a later period. François Franck and Pitres‡ have shown that a distinct interval elapses between the application of a stimulus to the brain and the movement induced by it—an interval amounting to about 1·22nd of a second when the requisite deductions are made for latent periods in nerve and muscle, and for the rate of transmission of nervous impulses in the cord and nerves. After removal of the grey matter, if the stimulus be applied to the medullary fibres, the period of retardation diminishes to about 1·33rd of a second, which proves that the grey matter constitutes not a conductor but a centre. Fritsch and Hitzig§ are of opinion that the cortical centres are related to the muscular sense, on the ground that after the ablation of the limb-centres in dogs, the animals so operated on do not suffer from paralysis of the limbs, but merely appear to have lost consciousness of the position of the limbs, and hence place them in irregular and unnatural attitudes. This view is also supported by Nothnagel from the results of his experiments in the injection of chromic acid into the brain cortex.‖ A very different view of the functions of the cerebral cortex is entertained by Goltz.¶ According to this observer, every part of the grey matter of the substance of the hemispheres participates in the exertion of the will, in the perception of sensations,

* See Albertoni and Michieli, "Sperimentale," vol. xxxvii. 1876; Firenze., Dupuy, "Examen de quelques points de la Physiologie du Cerveau," 1873; Thése, "Researches into the Physiology of the Brain," New York, 1878; Franck and Pitres, "Soc. de Biologie," Dec. 23, 1877; "Gazette Hebdomad," 1878, No. 1.

† Soltmann, "Centralblatt f. d. Med. Wiss.," 1875, p. 209; and "Jahrb. f. Kinderheilk," N. F. ix. p. 106. ‡ Loc. cit.

§ See also Schiff, "Archiv f. Exp. Pathol. und Pharmacol.," 1874, Band iii.

‖ Nothnagel (Virchow's "Archiv," Band lvii. p. 184, and lviii. p. 420) found on injecting a solution of chromic acid into a point about 14 mm. (half an inch) from the anterior extremity of the cerebral hemisphere in rabbits, and about 1-12th of an inch from the median fissure, that the opposite fore-paw dragged in walking, and could be placed in the most awkward positions without the animal resenting it, or attempting to withdraw it. It was, however, neither insensible nor paralyzed, it only appeared to have lost its muscular sense. A similar spot influencing both the fore and hind legs exists at the outer extremity of the gyrus post-frontalis. The affection is transitory, and disappears in a few weeks. Other motor paralyses were observed with injections made into various parts of the white substance. He finds a spot near the middle and inner part of the corpus striatum, which when injured leads in a course of a few minutes to violent leaping and springing forward movements, which continue for a quarter or half an hour till the animal drops exhausted; he terms this spot the *nodus cursorius*. Injury to a spot situated at the posterior extremity of the single sulcus of the brain of the rabbit is followed by similar springing movements, which after a few minutes cease entirely. Nothnagel found that ablation or destruction of the lenticular nucleus was followed by the same effects as removal of the cerebral hemisphere of the same side. See also Fournié, "Comptes Rend.," t. lxxvii. No. 5.

¶ Pflüger's "Archiv," 1879, p. 40; see also Hermann, idem, Band x.

in the conception of ideas, and in the exercise of thinking. Every segment, independently of the rest, is connected by strands with all the voluntary muscles, and by other strands or conductors with all the sensory nerves of the body. Goltz wholly denies the existence of small circumscribed and associated centres for the various groups of muscles or regions of the skin. The cortex of the brain acts as a whole, thinks as a whole, orders movements as a whole; though no doubt there are certain channels through which the influence of the will is conducted to the lower co-ordinating centres. He points out that in the case of the spinal cord, the structure and functions of which are far more simple than that of the brain, division temporarily abolishes the activity of the distant part, but that after a time, as may be observed in frogs and in dogs, the several reflex acts of micturition, defæcation, and even of those implicated in the performance of the sexual functions, are re-established—a result that is certainly not due to the reunion of the divided parts. The temporary failure of the functions of the lower segment after the operation of division, he attributes to an inhibitory influence being exerted on its grey matter by the irritation of the cut surface during the process of healing. But if this occur in the case of the spinal cord, much more is such an inhibitory influence likely to be exerted after ablation of large portions in an organ so complex as the brain. Hence, he argues, little weight is to be attached to the fact that paresis, or even abolition of the power of performing certain movements or of perceiving certain sensations, follows serious lesion of a particular region of the surface of the hemisphere. In many cases the effects observed are not constant, and even when well marked at first are quite transient; and he has satisfied himself that after extensive injury of various parts of the cerebral cortex, the animal does not lose special powers, as would be the case were there definite psychic centres, but is only rendered generally duller, less sensitive to external impressions, and more indisposed to exertion of any kind than before. The interpretation which Ferrier puts upon his experiments differs essentially from either of the foregoing. He regards the movements which result from stimulation as indications of excitation of centres concerned in voluntary or purposive action, or of centres of expression and sensation. The motor portion of the brain is situated anteriorly, and corresponds with the medullary expansion of the fibres from the corpus striatum, while the sensory portion corresponds with the medullary expansion from the optic thalamus. The destruction of a motor centre causes paralysis of voluntary motion in respect to the actions which are excited by stimulation of the same centre. This paralysis, however, is only complete in cases of movements which are quite independent of each other. It is seen more especially in the case of the monkey, which, like man, is capable of highly complex and independent movements. In dogs and quadrupeds generally, owing to the fact of the movements being automatically organized on both sides, the destruction of a motor centre in one hemisphere does not cause complete paralysis. Under the influence of the other hemisphere, or in response to sensory stimuli, action of both sides may be caused by the agency of the lower ganglia. Hence a dog may rapidly recover from the paralysis of motion, which manifests itself immediately after the destruction of the motor centres in the opposite hemisphere. This explanation is in accordance with the theory of Dr. Broadbent, who accounts for the fact that paralysis from brain disease affects the arm more than the leg, owing to the bilateral co-ordination in each hemisphere of movements usually associated together. Hence the motor centres in the brain are regarded by Ferrier as the differentiated apparatus of voluntary muscular action. At the same time they form what he terms the motor substrata of intellect, by being the centres of memory of muscular actions. Hence he

explains how the loss of speech is associated with the destruction of that part of the brain which is the centre for the movements of articulation.

523. As regards *sensory localization*, Ferrier, from a series of experiments on monkeys, claims to have localized the regions of special sense. These regions he regards as the centres of sensory perception, and as distinct from the centres for sensory impressions or sensori-motor action. The following is an abstract of these later researches, in which also attempts have been made to ascertain the functions of those parts of the hemispheres which do not react to stimulation:*—1. Ablation of the frontal regions which give no reaction to electrical stimulation is without effect on the powers of sensation or voluntary motion, but causes marked impairment of intelligence and of the faculty of attentive observation. 2. Destruction of the grey matter of the convolutions bounding the fissure of Rolando, causes paralysis of voluntary motion on the opposite side of the body; while lesions circumscribed to special areas in those convolutions, previously localized by the author, cause paralysis of voluntary motion, limited to the muscular action excited by electrical stimulation of the same parts. 3. Destruction of the angular gyrus (*pli courbe*) causes blindness of the opposite eye, the other senses and voluntary motion remaining unaffected. This blindness is only of temporary duration, provided the angular gyrus of the other hemisphere remain intact; when both are destroyed, the loss of visual perception is total and permanent.† 4. The effects of electrical irritation and the results of destruction of the superior temporo-sphenoidal convolution indicate that they are the centres of the sense of hearing. 5. Destruction of the hippocampus major and hippocampal convolution abolishes the sense of touch on the opposite side of the body. 6. The sense of smell (for each nostril) has its centre in the subiculum cornu Ammonis or tip of the uncinate convolution on the same side. 7. The sense of taste is localized in a region in close proximity to the sense of smell, and is abolished by destructive lesion of the lower part of the temporo-sphenoidal lobe. (The action is crossed.) 8. Destruction of the optic thalamus causes complete anæsthesia of the opposite side of the body. 9. Ablation of the occipital lobe produces no effect on the special senses or on the powers of voluntary motion, but is followed by a state of depression and refusal of food not to be accounted for by mere constitutional disturbance consequent on the operation. The function of these lobes is regarded as still obscure, but considered as in some measure related to the systemic sensations. Their destruction does not abolish the sexual appetite. 10. After removal both of the frontal and occipital lobes, an animal still retains its faculties of special sense and the power of voluntary motion. In the experiments made by the committee of the New York Society of Neurology and Electrology, including Drs. Dalton, Arnold, Beard, Flint, and Mason,‡ results confirmatory of Hitzig's observations were met with. They found that all the centres of motion for the anterior and posterior limbs are situated in the convolution immediately surrounding the frontal fissure which runs transversely to the longitudinal fissure. The centres for flexion and extension of the anterior and posterior limbs were always found in the external part of the præ-frontal convolution just anterior to this fissure, and in the post-frontal convolution just behind it. In a majority of cases, those for the anterior limbs were situated more in front, near the outer extremity of the frontal fissure, and those for the posterior limbs more posteriorly and inwards,

* "Experiments on the Brain of Monkeys," second series, read before the Royal Society, May 13, 1875. Abstract of Croonian Lecture.

† See Luciani and Tamburini, "Centralblatt f. d. Med. Wiss.," 1879, p. 677.

‡ "New York Med. Journ.," March, 1875.

but their exact positions varied somewhat in different cases. The centre for flexion of the head and neck in the median line is in the lateral and anterior part of the præ-frontal convolution, where it leads downwards and outwards; that for flexion of the head with rotation towards the side of the stimulus is in a part of the convolution situated still farther towards the front and downward, so as to be invisible in a view of the brain taken from above. The centre for the facial muscles is in a region situated on the lateral part of the hemisphere immediately above the supra-Sylvian fissure.* Munk† divides the brain of Dogs into an anterior or motor, and a posterior or sensory portion, separated from each other by a vertical line passing from the end of the fissure of Sylvius to the Falx. Lesion of the posterior superior extremity of the occipital lobe causes *psychic* blindness; lesion of the inferior part of the temporal lobe causes *psychic* deafness. In both instances there is loss of memory of the visual or auditory images, so that it no longer knows or recognizes what it sees or hears, though it does both see and hear. This condition, however, is only temporary. Munk thinks the visual sphere is localized in the cortex of the occipital lobes (and not, as Ferrier believes, in the angesta gyrus) in such a way that each retina is co-ordinated by its outermost and lateral part with the outermost and lateral part of the corresponding hemisphere. The remaining and much larger part of the retina lay associated with the vesical spleen of the cortex of the opposite occipital region. Eulenburg and Landois‡ and Hitzig§ have noticed that the ablation or destruction of regions in close proximity to Hitzig's and Ferrier's motor centres is followed by exaltation of temperature in the opposite hind-leg, which may amount to as much as 13° C. ($23\frac{2}{5}$° F.), and which may last for a day or two only, or may persist for three months. Electrical stimulation of this region lowered the temperature of the limbs of the opposite side. It thus appears probable that the mind can exert an influence upon the temperature of particular parts of the body.‖ It may also be noticed that strong stimulation of the motor centres of the extremities, according to Bochefontaine,¶ causes increase of the blood pressure in the arteries and retardation of the beats of the heart, and this occurs even after division of the vagi and sympathetics in animals.

524. The effects of the entire removal of the Cerebral Hemispheres have been already stated.** So far as any inferences can be safely drawn from them, these experiments fully bear out the conclusion that the Cerebrum is the organ of Intelligence; since the animals which have suffered this mutilation appear to be plunged in a profound sleep, from which no irritation ever seems able to rouse them into full activity, although they give manifestations of consciousness. It would be wrong hence to infer, however, as some have done, that such would be the natural condition of an animal without a Cerebrum; since it is obvious that much of the disturbance of the sensorial powers which is occasioned by this operation, is fairly attributable to the laying open of the cranial cavity, to the disturbance of the normal vascular pressure, and to the injury necessarily done to the parts which are left by their severance from the Cerebrum. Hence the persistence of consciousness after the entire removal of the Cerebrum—which

* For other recent researches on this subject see Beaunis, "Gazette Médicale de Paris," No. 30, 1872. Fournié, "Récherches Expérimentales," 1873. Crichton Brown, "Brit. Med. Journ.," 1875, p. 447.

† See "Verhandl. d. Physiolog. Gesells. zu Berlin," 1876-7-8-9.

‡ "Centralblatt f. d. Med. Wiss.," 1876, p. 260; "Archiv f. Pathol. Anat.," Band lxviii. p. 245, and "Comptes Rendus," lxxxii. p. 564.

§ "Centralblatt f. d. Med. Wiss.," 1876, p. 323.

‖ Landois, "Lehrbuch der Physiologie," 1880, p. 754. ¶ "Comptes Rendus," lxxxiii. p. 233.

** For a good Memoir on this subject, reference to which was accidentally omitted, see Lautenbach, "Amer. Jour. Med. Sci.," Oct. 1877.

proves that the Cerebrum is *not* its seat, or at least *not its exclusive* seat—is a far more important fact than the positive destruction of psychical power which is consequent upon the operation. So far as they can be trusted, however, the results of such mutilations bear out the views already put forth, as to the superadded and non-essential character of the Cerebrum; and justify us in applying to the higher animals the inferences to which we should be led by the contemplation of those forms of the nervous system in which no Cerebrum exists. There is nothing, therefore, to oppose the conclusion, that whilst *sensations* may be felt, and sensori-motor actions excited, independently of the Cerebrum, the presence of this organ is essential to the formation of *ideas* or notions respecting the objects of sense, and to the performance of those psychical operations for which ideas furnish at once the material and the stimulus to activity.

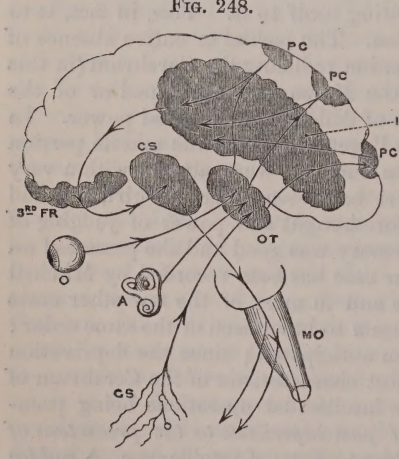
525. The information afforded by Pathological phenomena is far from being definite.* Many instances are on record in which extensive disease has occurred in *one* Hemisphere, so as almost entirely to destroy it, without either any obvious injury to the mental powers, or any interruption of the influence of the mind upon the body. But there is no case on record of any such severe lesion of *both* hemispheres, in which morbid phenomena were not evident during life. It is true that, in Chronic Hydrocephalus, a very remarkable alteration in the condition of the Brain sometimes presents itself which might *à priori* have been supposed destructive to its power of activity; the ventricles being so enormously distended with fluid, that the cerebral matter has seemed like a thin lamina spread over the interior of the enlarged cranium. But there is no proof that absolute destruction of any part was thus occasioned; and it would seem that the very gradual nature of the change gives to the structure time for accommodating itself to it. This, in fact, is to be noticed in all diseases of the Encephalon. The partial or entire absence of the commissures from congenital malformation reducing the Cerebrum (in this respect) at least, to the level of that of the Marsupial Quadruped or of the Bird is by no means an unfrequent cause of deficient intellectual power. In an interesting case recorded by Sir James Paget,† in which the middle portion of the fornix and the whole of the septum lucidum were absent, with a very thin and short corpus callosum, the subject had been a servant-girl, and had during life betrayed a peculiar want of forethought and power of judging of the probable result of things, but her memory was good and she possessed an ordinary amount of knowledge. A similar case has been recorded by Mitchell Henry.‡ The mental deficiencies in this and in most of the few other cases of which the details have been recorded, seem to have been of the same order; and this is exactly what might have been anticipated; since the deprivation of these parts takes away that which is most characteristic of the Cerebrum of Man and of the higher Mammalia; *their* intellectual operations being peculiarly distinguished by that *application of past experience to the prediction of the future*, which constitutes one of the highest efforts of intelligence. A *sudden* lesion, that may be so trifling as to escape observation unless this be very carefully conducted, will occasion very severe symptons; whilst a chronic disease may gradually extend itself, without any external manifestation. It will usually be found that sudden paralysis, of which the seat is in the Brain, results from some slight effusion of blood in the substance or in the neighbourhood of the Corpora striata; whilst, if it follows disorder of long standing, a much greater amount of lesion commonly presents itself. In either case, the paralysis occurs in the opposite side of the *body*, as we should expect from the decussation of

* For abundant evidence on this point see M. Brown-Séquard, "Archives of Scient. and Pract. Med.," vol. i. 1873, p. 255; Kahler and Pick, "Präger Vierteljahrschrift," N. F., 1879, Heft 1 and 2. † "Med.-Chir. Trans.," vol. xxiv. ‡ Op cit., vol. xxxi.

the Pyramids; but it may occur either on the same, or on the opposite side of the *face*—the cause of which has already been explained. The disturbance of the Cerebral functions occasioned by those changes in its nutrition which are commonly included under the general term Inflammation, presents a marked diversity of character according to the part it affects. Thus it is well known that the Delirium of excitement is usually a symptom of inflammation of the cortical substance or of the membranes of the Hemispheres. This is exactly what might be anticipated from the foregoing premises, since this condition is a perversion of the ordinary mental operations, which are dependent upon the instrumentality of the vesicular matter; and it is evidently impossible for the membranes to be affected with inflammation, without the nutrition of this substance being impaired, since it derives all its vessels directly from them. On the other hand, inflammation of the fibrous portion of the Cerebrum is usually attended rather with a state of torpor than with excitement; and with diminished power of the will over the muscles. It is stated by Foville, that in acute cases of Insanity he has usually found the cortical substance intensely red, but without adhesion to the membranes; whilst in chronic cases it is indurated and adherent: but where the insanity has been complicated with paralysis, he has usually found the medullary portion indurated and congested.

526. The numerous and interesting observations which have been made during the last few years on loss of the faculty of language, or rather of intellectual expression,* are of great interest in reference to the Physiology of the Brain. It is commonly associated with Right Hemiplegia, and in a large proportion of the cases examined after death, disease has been found in the posterior part of the third or inferior frontal convolution of the left hemisphere; hence the conclusion has been drawn that the faculty of language has its seat in this particular convolution. Language, however, is co-extensive with thought, and the third left frontal convolution is not the seat of language as a faculty of the mind, but is simply an important link in the nervous mechanism of speech. Dr. Hughlings Jackson† has pointed out that language may be intellectual or emotional, and that when all power of expressing ideas in words is lost, an entire phrase may be uttered under emotion. Intellectual language again, or intellectual expression, he shows to be a department of educated movements in general, and gives reasons for believing that the entire hemisphere is concerned in its evolution. It conflicts with all preconceived notions that the left side of the brain should alone have to do with the expression of ideas in language, but this seems to be clearly demonstrated by Pathology. P. Broca and Dr. Moxon have explained it by supposing that one

Fig. 248.



A. Auditory nerves. O. Optic nerve. G S. General sensory surface. O T. Optic thalamus. P C. Perceptional centre. I C. Ideational centre. C S. Corpus striatum. 3 F R. Third frontal convolution. M O. Medulla oblongata.

* See Aphasia, Agraphia, &c., in the Year Books of the New Sydenham Society.

† "Lancet," Feb. 1866, Dec. 1867, July and Nov. 1868.

side of the brain only is educated, and Gratiolet's observation that the left frontal convolutions are developed before the right, has been adduced in support of this view, which, however, cannot be said to be established. The mechanism of speech and thought may be represented as follows. Impressions derived from sensory surfaces generally (G S, Fig. 248) and from the organs of special sense (O A), are translated in the sensory ganglia of the base of the brain (O T) into sensations. These sensations transmitted upwards to the cortex of the hemispheres here give rise to perceptions, that is, to the intellectual recognition of the external causes of the sensations; by combination again of the different perceptions derived from a given object, an idea or complete intellectual representation of the object is formed, with which is associated a name. The "perceptive centres" (Bastian) in which simple perceptive recognition takes place (P C) are probably situated near the margins of the hemisphere where the convolutions are directly connected by fibres with the central ganglia, while ideas are supposed to be formed in the convolutions remote from the margins, many of which receive no fibres from the central ganglia or crus, but are connected by arcuate fibres with the marginal convolutions and with each other. Up to the present the mechanism described is that concerned in the reception of impressions and the formation and association of ideas. When these ideas are to be expressed in words, the proposition is formulated, and the phrase mentally rehearsed in the higher convolutions, and transmitted for verbal expression to the third left frontal gyrus, the function of which is to provide the appropriate words or motor symbols in which the idea is to be clothed, and call into action through the corpus striatum the motor nerve-nuclei in the medulla which are concerned in articulation and phonation. The third left frontal convolution is thus the first step on the way out for words, and damage here leaves the subject of it able on the one hand to understand what is said, to form ideas, and even to rehearse propositions in his mind, and on the other hand able to execute all the movements required for articulation and phonation, though from the breach in the mechanism for translating ideas into words, he is speechless. This is pure Aphasia, but cases uncomplicated by further damage are rare, while speechlessness of a totally different character is often confounded with Aphasia. The nervous mechanism may, in fact, be injured at different points. Below the third frontal convolution, lesion in the Corpus striatum may cause impairment of articulation, or in the medulla or its nerves, more or less complete loss both of phonation and articulation (*alalia*). Here the speechlessness is simply from motor paralysis, but other forms of speechlessness arise from lesions in the cerebral or mental mechanism. Cases have been met with in which a man could speak and write correctly while unable to read a single word even of what he had himself written, or to name the most familiar object shown to him; the association by which the visual perception called up the name was broken. Let the association between the auditory perception and the name be similarly broken, and we have the explanation of the perplexing cases* in which a patient has lost all comprehension of articulate sounds, and neither understands what is said to him nor what he says, while he responds promptly to signs and appears to be intelligent. These are forms of Amnesia or loss of memory for words, but there are other more common forms of Amnesia in which a patient understands spoken words, but cannot recall them mentally so as to rehearse a phrase or proposition in his mind. Very frequently a degree of Amnesia is associated with Aphasia, the various degrees and combinations of loss of

* See Broadbent, "Med.-Chir. Trans.," 1872–5, to whom the Editor is indebted for aid in drawing up this section, and for the Figure by which it is illustrated.

memory for words and loss of memory how to say words depending upon the region and extent of cortex involved, or upon the severance of fibres connecting together different sets of convolutions. Again, in extensive disease of the Cortex there is no speech because there is no idea; this is dementia or mutism.

527. The general result of pathological investigation is, that the Cerebrum is the instrument of all those *psychical* operations, which we include under the general term *Intellectual*, whilst it also affords, in part at least, the instrumental conditions of *Emotional* states; and that all those muscular movements which result from *voluntary* determinations, or which are directly consequent upon *emotional* excitement, have their origin in its vesicular substance, though the motor impulse is immediately furnished by the Cranio-Spinal apparatus, upon which the Cerebrum plays (§ 524). It does not hence follow, however, that the Cerebrum has such a direct relation to the Mind, that the consciousness is immediately and necessarily affected by changes taking place in its own substance; and, however startling the proposition may at first sight appear, that the organ of the intellectual operations is not itself endowed with consciousness, a careful consideration of the relations of the Cerebrum to the Sensory ganglia will tend to show that there is no *à priori* absurdity in such a notion. For if the connection of the vesicular matter of the Cerebral hemispheres with the Sensorial centres be anatomically the same as that which exists between these centres and the Retina or any other peripheral expansion of vesicular matter in an organ of sense, which we have seen that it is—and if the same kind of change may be excited in the Sensorial centres by an impression from each source, which has been shown to be a matter of common occurrence—it can scarcely be deemed unlikely that the Sensorial centres should be the seat of consciousness, not merely for the impressions transmitted to them by the nerves of the external senses, but also for the impressions brought to them by the 'nerves of the internal senses,' as we may designate (after Reil) the radiating fibres of the Cerebral hemispheres. And there is on the other hand an *à priori* improbability that there should be *two* seats of consciousness, so far removed from one another as the Sensory ganglia and the vesicular surface of the Hemispheres (for to their medullary substance no such attribute can be assigned with the least probability); an idea which is quite at variance with that very simple and familiar class of phenomena, which consists in the *recollections of sensations*. For the remembered sensation is so completely the reproduction of the original, that we can hardly suppose the seat of the two to be different; yet the act of recollection is clearly Intellectual, and therefore Cerebral; consequently, if we admit that the Sensory ganglia are the seat of the original sensation, we can scarcely but admit that they are also the seat of that which is reproduced by the Cerebral act—a view which is fully confirmed by the occurrence of automatic movements as consequences of its recall. And a careful analysis of our own mental operations will often supply evidence of the evolution of results, such as ordinarily proceed from intellectual action, without any consciousness on our own parts of the steps whereby these are attained. Without presuming, then, to affirm positively what cannot be proved, it may be stated as a probable inference from the facts already referred to, that the Sensory ganglia constitute the seat of consciousness, not merely for impressions on the Organs of Sense, but also for changes in the cortical substance of the Cerebrum; so that, until the latter have reacted downwards upon the Sensorium, we have no consciousness either of the formation of ideas, or of any intellectual process of which these may be the subjects.—Ideas, Emotions, Intellectual operations, &c., have of late been frequently designated as 'states

of consciousness;' and this psychological description of them is in full harmony with the physiological account here given of the material conditions under which they respectively occur. For as a Sensation is a state of consciousness excited through the instrumentality of the Sensorium, by a certain change—*e.g.*, in the condition of the Retina—it is not difficult to understand how a change in the condition of the Cerebrum may excite, through the same instrumentality, that state of consciousness which may be termed Ideational,* or that another change may produce the Emotional consciousness, another the Intuitional consciousness, another the Logical consciousness. And although it may be thought at first sight to be a departure from the simplicity of Nature to suppose that the Cerebrum should require another organ to give us a consciousness of its operations, yet we have the knowledge that the Eye does not give us visual consciousness, nor the Ear auditory consciousness, unless they be connected with the Sensory ganglia; and in the end (the Author feels a strong assurance) it will be found much simpler to accept the doctrine of a common centre for *sensational*, and for what may be distinguished as *mental* consciousness, than to regard the two centres as distinct.†

6. *Of Sleep and Somnambulism.*

528. It is a peculiar feature in the physiology of the Cerebral and Sensorial ganglia, that their activity undergoes a periodical suspension more or less complete; the necessity for this suspension arising out of the fact that the exercise of their functions is in itself destructive to their substance, so that, if this be not replaced by nutritive regeneration, they speedily become incapacitated for further use. An ingenious theory of the *cause* of sleep has been advanced by Sommer,‡ founded on the observations of Pettenkofer and Voit already alluded to (§ 287, viii.). Sommer observes that if, as the experiments of Pettenkofer appear to show, oxygen is gradually being stored up during sleep, a period will probably arrive when it exists in such excess as materially to accelerate the metamorphosis of the nervous and other tissues, and as a consequence awakening occurs. On the other hand, during the waking state the stored-up oxygen is gradually eliminated, as shown by the large proportion of carbonic acid given off, until at length, when all the excess has been consumed, exhaustion and general relaxation is experienced, accompanied by the desire for sleep. This view has been expressed at considerable length by Pflüger,§ who suggests that the waking state is maintained by the violent oscillations, almost comparable to small explosions, taking place in the molecules of the cerebral substance, owing to the combination of the intra-molecular oxygen with the carbon of the tissue. These vibrations radiate outwards far and wide along the nerves in all directions. As the oxygen is gradually used up, the explosions become feebler, the activity of all nervous processes less, mental operations are conducted with less energy, the exhausted and quiescent nerves are no longer easily aroused by impressions from without, and sleep results. On Dr. Cappie's‖ theory, the links in the causation of sleep are, first,

* The Author ventures to use this term, the meaning of which requires no explanation, on the authority of Mr. James Mill, who remarks:—"As we say Sensation, we might also say Ideation; it would be a very useful word, and there is no objection to it, except the pedantic habit of decrying a new term. Sensation is the general name for one part of our constitution [or rather, for one state of our consciousness], Ideation for another." ("Analysis of the Human Mind," vol. i. p. 42.)—If the use of the substantive Ideation be admitted, there can be no reasonable objection to the adjective *ideational*.

† An interesting and suggestive paper by Mr. Lockhart Clarke, 'On the Nature of Volition,' will be found in Nos. 7, 8, and 9 of the "Psychological Journal" for 1862.

‡ Henle and Pfeuffer's "Zeits. f. Rat. Med.," Band xxxii. 1868, p. 214.

§ Pflüger's "Archiv," 1875, p. 468. ‖ Cappie, "The Causation of Sleep," 1872, p. 32.

that there is diminished molecular activity of the cerebral cells, whilst coincidently there is a change in the capillary circulation of the brain, so that less blood is supplied to it, and it consequently occupies less space. But as the brain-case must be constantly full, the veins of the pia mater undergo gradual and proportional distension, and although the absolute quantity of blood and the amount of internal pressure remain unaltered, the direction of the pressure is modified. It is less from within, and more on the surface of the organ, and with altered direction of pressure the continued exercise of function is incompatible. This view is quite in accordance with the interesting researches of Mr. Arthur Durham* on the condition of the circulation in the Brain during sleep, which have shown that the brain is then in an essentially bloodless condition, and that not only the quantity but the rapidity of movement of the blood in the vessels is materially diminished; and this is corroborated by the observations of Dr. J. Hughlings Jackson on the ophthalmoscopic condition of the Retina during sleep,† the optic disc being then whiter, the arteries smaller, the veins somewhat larger, and the neighbouring part of the retina more anæmic, than in the waking state. In ordinary profound Sleep there is a state of complete unconsciousness, so far as *external* phenomena are concerned; no ordinary impressions upon the organs of sense being either felt or perceived; although an extraordinary impression, or even an habitual one upon which the attention has been previously fixed as that at which the slumberer is to awake himself (§ 534), occasions a renewal of activity. It is in this capability of being aroused by external impressions that the chief difference lies between Sleep and the abnormal condition of Coma, whether this arise from the influence of pressure or effusion within the cranium, or be consequent upon the poisoning of the blood by narcotic substances, or follow a previous state of abnormal activity of the brain, such as Delirium. Between these two conditions, however, every gradation may be seen; as in the gradually increasing torpor which results from slow effusion within the cranium, the gradual loss of susceptibility to external impressions which is observed on the application of cold to the nervous centres, as in the interesting experiments of Dr. Richardson and Dr. Weir Mitchell,‡ or after an overdose of a narcotic, as well as in the intensification of ordinary sleep which is consequent upon extreme previous fatigue. But it is a matter of doubt whether the suspension of sensorial consciousness is equally complete as regards *internal* or cerebral changes; for some are of opinion that, even in the most profound sleep, we still dream, although we may not remember our dreams; whilst others (and among these the Author would rank himself) consider that dreaming is a mark of imperfect sleep, and that, in profound ordinary sleep, the Cerebrum, in common with the Sensory ganglia, is in a state of complete functional inactivity. When Dreaming takes place, there is usually a less complete exclusion of sensory impressions, although the perceptive consciousness may be entirely suspended; so that the course of the dream may be influenced by them, although the mind is not conscious of them as such (§ 538). If this be the true account of the case, we may consider that in profound Sleep the functional activity of the Cerebrum and of the Sensory ganglia is alike suspended; but that in Dreaming the Cerebrum is partially active, whilst the Sensorium is in such a condition of receptivity for Cerebral (subjective) impressions that the mind becomes directly conscious of them, though

* "Guy's Hospital Reports," Third Series, vol. vi.

† See "Royal Lond. Ophth. Hosp. Reports."

‡ See for Dr. Richardson's experiments, "Medical Times and Gazette," 1867, vol. i. p. 489, *et seq.*; and for those of Dr. Mitchell the "American Journal of Medical Science," 1867, p. 102.

it only becomes conscious of (objective) impressions made upon the Organs of Sense, after their influence has been transmitted through it to the Cerebrum, and has been, as it were, reflected back by that organ. It is, in fact, by their influence upon the current of *ideas*, and not by their power of exciting *sensations*, that we recognise their operations under such circumstances.

529. The state of sleep is one to which there is beyond doubt a *periodical* tendency; for, when the waking activity has continued during a considerable proportion of the twenty-four hours, a sense of fatigue is usually experienced, which indicates that the brain requires repose; and it is only under some very strong physical or moral stimulus that the mental energy can be maintained through the whole cycle. In fact, unless some decidedly abnormal condition of the Cerebrum be induced by the protraction of its functional activity, Sleep will at last supervene, from the absolute inability of the organ to sustain any further demands upon its energy, even in the midst of opposing influences of the most powerful nature.* That the strongest volitional determination to remain awake is forced to give way to Sleep, when this is required by the exhaustion of nervous power, must be within the experience of every one; and the only way in which the Will can even retard its access, is by determinately fixing the consciousness upon some definite object, and resisting every tendency in the thoughts to wander from this. It does not appear to be of any consequence whether this exhaustion be produced by the active exercise of volition, reflection, emotion, or simple sensation; still we find that the *volitional* direction of the thoughts in a course different from that in which they tend spontaneously to flow, is productive of far more exhaustion than the automatic activity of the mind; whilst, on the other hand, the excess of *automatic* activity, whether as regards the intellectual operations or emotional excitement, tends to prevent sleep. This is particularly the case when the feelings are deeply interested; thus the strong desire to work out a result, or to complete the survey of a subject, is often sufficient to keep up the intellectual activity as long as may be requisite (a state of restlessness indeed being often induced, which prevents the access of sleep for some time longer); so, again, anxiety or distress is a most frequent cause of wakefulness; and it is generally to be observed that the state of *suspense* is more opposed to the access of sleep than the greatest joy or the direst calamity when certainty has been attained.† But although an excess of automatic activity is opposed, so long as it continues, to the access of sleep, yet it cannot be long protracted

* Thus it is on record, that during the heat of the battle of the Nile, some of the overfatigued boys fell asleep upon the deck: and during the last attack upon Rangoon, the Captain of one of the war-steamers most actively engaged, worn-out by the excess of continued mental tension, fell asleep, and remained perfectly unconscious for two hours, within a yard of one of his largest guns, which was being worked energetically during the whole period.—So even the severest bodily pain yields before the imperative demand occasioned by the continued exhaustion of the powers of the sensorial centres; thus Damiens slept upon the rack, during the intervals of his cruel sufferings; the North American Indian at the stake of torture will go to sleep on the least remission of agony, and will slumber until the fire is applied to awaken him; and the Medical Practitioner has frequent illustrations of the same fact.—That the continued demand for muscular activity is not incompatible with the access of sleep, is obvious from what has been already said of the persistence of the automatic movements in that condition; it is well known that, previously to the shortening of the hours of work, factory children frequently fell asleep whilst attending to their machines, although well aware that they would incur severe punishment by doing so.

† Thus it is a common observation, that criminals under sentence of death sleep badly so long as they entertain any hopes of a reprieve; but when once they are satisfied that their death is inevitable, they usually sleep more soundly, and this even on the very last night of their lives.

without occasioning an extreme exhaustion of nervous power, which necessitates a long period of tranquility for its complete restoration. Whilst, however, the necessity for Sleep arises out of the state of the nervous system itself, there are certain external conditions which favour its access; and these, in common parlance, are termed its predisposing causes. Among the most powerful of these, is the *absence* of sensorial impressions; thus, darkness and silence usually promote repose; and the cessation of the sense of muscular effort, which takes place when we assume a position that is sustained without it, is no less conducive to slumber. That sleep ensues when all stimuli to cerebral activity are withdrawn, is remarkably shown by a case recorded by Dr. Strümpell.* In this instance, a girl of sixteen years of age became almost completely anæsthetic, being unable to perceive the most violent stimulation of the skin and mucous membranes, losing the muscular sense, and even the sense of muscular fatigue, and preserving her relation with the outer world by two channels only—the right eye and the left ear. It was found that on applying a bandage to the eye and plugging the ear, she fell in the course of two or three minutes into a deep sleep. She could be awaked from this by the application of the natural stimulus either to the ear or eye, though if allowed to sleep for several hours, waking occurred naturally, apparently from the action of certain internal stimuli. There are cases, however, in which the *continuance* of an accustomed sound is necessary, instead of positive silence, the cessation of the sound being a complete preventive of sleep; thus it happens that persons living in the neighbourhood of the noisiest mills or forges cannot readily sleep elsewhere. Such cases are referable either to the influence of *habit*, which causes the attention of the individual to be more attracted by the suspension of the sound than by its continuance; or to the fact that the *monotonous repetition* of sensorial impressions is often more favourable to sleep than their complete absence. Thus it is within the experience of every one, that the droning voice of a heavy reader on a dull subject is often a most effectual hypnotic; in like manner, the ripple of the calm ocean on the shore, the sound of a distant waterfall, the rustling of foliage, the hum of bees, and similar impressions upon the auditory sense, are usually favourable to sleep; and the muscular and tactile senses may be in like manner affected by an uniform succession of gentle movements, as we see in the mode in which nurses 'hush off' infants, or in the practice of gently rubbing some part of the body which has been successfully employed by many who could not otherwise compose themselves to sleep. The reading of a dull book acts in the same mode through the visual sense; for the eyes wander on from line to line, and from page to page, receiving a series of sensorial impressions which are themselves of a very monotonous kind, and which only tend to keep the attention alive in proportion as they excite interesting ideas.

530. In these and similar cases the influence of external impressions would seem to be exerted in withdrawing the mind from the distinct consciousness of its own operations (the loss of which is the transition state towards that of complete unconsciousness), and in suspending the directing power of the Will. And this is the case, even where the attention is in the first instance *voluntarily* directed to them; as in some of the plans which have been recommended for the induction of sleep, when there exists no spontaneous disposition to it. In other methods, the attention is fixed upon some internal train of thought, which, when once set going, may be carried on automatically; such as counting numbers, or repeating a French, Latin, or Greek verb. In either case, when the sensorial consciousness has been once steadily fixed, the monotony of the

* Pflüger's "Archiv," Band xv. 1877, p. 573.

impression (whether received from the Organs of Sense, or from the Cerebrum) tends to retain it there; so that the Will abandons, as it were, all control over the operations of the mind, and allows it to yield itself up to the soporific influence. This last method is peculiarly effectual when the restlessness is dependent upon some mental agitation; provided that the Will has power to withdraw the thoughts from the exciting subject, and to reduce them to the tranquillizing state of a mere mechanical repetition. The access of Sleep is sometimes quite sudden; the individual passing at once from a state of complete mental activity to one of entire torpor. More generally, however, it is gradual; and various intermediate phases may be detected, some of which bear a close resemblance to the state of Reverie. The same may be said with regard to the transition from the state of Sleep to that of wakeful activity; and this also may be sudden and complete, although it usually consists of a succession of stages—the complete consciousness of the individual's relation to the external world, and the power of directing his thoughts and actions to any subject about which he may be required to exert himself, being the last to return to him. There may be a rapid alteration of these different states; the loss and recovery of the waking consciousness being many times repeated in the course of a few minutes, when the circumstances are such as to prevent the access of profound sleep by the recurrence of sensory impressions; as when a man on horseback, wearied from want of rest, lapses at every moment into a dozing state, from which the loss of the balance of his body as frequently and suddenly arouses him; or when a man going to sleep in a sitting posture, gradually loses the support of the muscles which keep his head erect, his head droops by degrees, and at last falls forward on his chest, and the slight shock thence ensuing partially arouses and restores his voluntary power, which again raises the head. Similar fluctuations occur in the sensory perceptions; and these may be often artificially induced by very simple means. "We find, for example, one condition of sleep so light, that a question asked restores consciousness enough for momentary understanding and reply; and it is an old trick to bring sleepers into this state, by putting the hand into cold water, or produce some other sensation, not so active as to awaken, but sufficient to draw the mind from a more profound to a lighter slumber. This may be often repeated, sleep still going on; but make the sound louder and more sudden, and complete waking at once ensues. The same with other sensations. Let the sleeper be gently touched, and he shows sensibility, if at all, by some slight muscular movement. A ruder touch excites more disturbance and motion, and probably changes the current of dreaming; yet sleep will go on; and it often requires a rough shaking, particularly in young persons, before full wakefulness can be obtained.". . . . "It is certain that the faculties of sensibility and volition are often unequally awakened from sleep. The case may be stated, familiar to many, of a person sleeping in an upright posture, with the head falling over the breast; in whom sensibility is suddenly aroused by some external impression, but who is unable, for a certain time, to raise his head, though the sensation produced by this delay of voluntary action is singularly distressing." These various cases, it is justly remarked by Sir H. Holland,* depending severally on the intensity of sleep, and on the kind and degree of the external exciting causes will be found to explain many of those so-called mesmeric phenomena, which are offered to us under a widely different interpretation. And it may be here remarked, that among those intermediate stages between sleep and waking, which either occur spontaneously, or can be

* See his excellent chapter on 'Sleep,' from which the above extracts are taken, in his "Medical Notes and Reflections," and his "Chapters on Mental Physiology."

induced in numerous individuals by very simple processes, there are several which exhibit peculiarities that are not in themselves in the least degree less remarkable, than are those which are regarded with so much wonder by the uninformed observer, when induced by the asserted mesmeric influence, and paraded as specimens of its power.

531. It is unquestionable that the supervention of sleep may be promoted by the strong previous expectation of it; and this is true, not merely of ordinary sleep, but of the states of artificial Reverie and Somnambulism formerly described. Everyone knows the influence of habit, not only in regard to 'time,' but also as to 'place and circumstance,' in predisposing to Sleep. Thus, the celebrated pedestrian, Captain Barclay, when accomplishing his extraordinary feat of walking 1000 miles in as many consecutive hours, obtained at last such a mastery over himself that he fell asleep the instant he lay down. And the sleep of soldiers, sailors, and others, who are prevented by 'duty' from obtaining regular periods of repose, but are obliged to take their rest at short intervals, may be almost said to come at command; nothing more being necessary to induce it, than the placing the body in an easy position and the closure of the eyes. It is related that the Abbé Faria, who acquired notoriety through his power of inducing somnambulism, was accustomed merely to place his patient in an arm-chair, and then, after telling him to shut his eyes and collect himself, to pronounce in a loud voice and imperative tone the word "dormez," which was usually successful. The Author has had frequent opportunities of satisfying himself, that the greater success which attended the 'hypnotic' mode of inducing somnambulism, in the hands of Mr. Braid, its discoverer, than in that of others, partly lay in the mental condition of his subjects who came to him for the most part under the confident expectation of its production, and were further assured by a man of very determined will, that it *could not* be resisted.* And it is one of the most curious phenomena of the state of induced Reverie, absurdly called 'biological,' that, in many subjects at least, sleep may be induced in a minute or less, by the positive assurance, with which the mind of the individual becomes possessed, that it *will* and *must* supervene.

532. The influence of previous mental states is yet more remarkable in determining the effects produced upon the sleeper by different sensory impressions. The general rule is, that *habitual* impressions of any kind have much less effect in arousing the slumberer, than those of a new or unaccustomed character. An amusing instance of this kind has been related to the Author, which, even if not literally true, serves extremely well as an illustration of what is unquestionably the ordinary fact. A gentleman who had taken his passage on board a ship of war, was aroused on the first morning by the report of the morning gun, which chanced to be fired just above his berth; the shock was so violent as to cause him to jump out of bed. On the second morning, he was again awoke, but this time he merely started and sat up in bed; on the third morning, the report had simply the effect of causing him to open his eyes for a moment, and turn in his bed; on the fourth morning, it ceased to affect him at all; and his slumbers continued to be undisturbed by the report, so long as he remained on board. It often happens that sleep is terminated by the *cessation* of an accustomed sound, especially if this be one whose monotony or continuous repetition had been the original inducement to repose. Thus, a person who has been read or preached to sleep, will awake, if his slumber be

* A very amusing instance in which Sleep, having been previously induced by the ordinary 'mesmeric' and then by the 'hypnotic' processes, was brought on by the simple belief that a new process was being put in practice, will be found in the "Brit. and For. Med. Rev.," vol. xix. p. 477.

not very profound, on the cessation of the voice; and a naval officer, sleeping beneath the measured tread of the watch on deck, will awake if that tread be suspended.—In this latter case the influence of the simple cessation of the impression will be augmented by the circumstance next to be alluded to, which has received too little attention from writers on this subject, but which is of peculiar interest both in a physiological and psychological point of view, and is practically familiar to almost everyone.

533. The awakening power of sensory impressions is greatly modified by our *habitual state of mind* in regard to them. Thus, if we are accustomed to *attend* to these impressions, and our perception of them is thus *increased* in acuteness, we are much more easily aroused by them, than we are by others, which are in themselves much stronger, but which we have been accustomed to disregard. Thus, most sleepers are aroused by the sound of their own names uttered in a low tone, when it requires a much louder sound of a different description to produce any manifestation of consciousness. The same thing is seen in comatose states; a patient being often found capable of being momentarily aroused by shouting his name into his ear, when no other sound produces the least effect.—The following circumstance, communicated to the Author by the late Sir Edward Codrington, is a most apposite illustration of this principle. When a young man, he was serving as signal-lieutenant under Lord Hood, at the time when the French fleet was confined in Toulon harbour; and being desirous of obtaining the favourable notice of his commander, he devoted himself to his duty (that of watching for signals made by the look-out frigates) with the greatest energy and perseverance, often remaining on deck nineteen hours out of the twenty-four, with his attention constantly directed towards this one object. During the few hours which he spent in repose, his sleep was so profound that no noise of an ordinary kind, however loud, would awake him; and it used to be a favourite amusement with his comrades, to try various experiments devised to test the soundness of his sleep. But if the word 'signal' was even whispered in his ear, he was instantly aroused, and fit for immediate duty.—The influence of habitual attention is shown as much in the effect produced by the cessation, as in that of the occurrence, of sensory impressions. Thus, in the case of the naval officer aroused by the suspension of the measured tread of the watch over his head, the knowledge possessed during the waking state, that this suspension is either an act of negligence which requires notice, or indicates some unusual occurrence, doubtless augments the effect which the discontinuance of the sound would of itself produce.

534. It is not requisite, however, that the sound should be one habitually attended to during the hours of watchfulness; for it is sufficient if it be one on which the *attention has been fixed* as that at which the slumberer is to arouse himself. Thus, the medical man, even in his first profound sleep after a fatiguing day's work, is aroused by the first stroke of the clapper of his night-bell; and to those who are accustomed to rise every morning at the sound of an alarum-clock, the frequency and regularity of the occurrence do not diminish, but rather increase, the readiness with which it produces its effects, provided that the warning be promptly obeyed. On this usually depends the efficiency of the awakening sound; if it be regarded as a thing to which there is no occasion to give heed, it very soon ceases to produce any effect, the entire peal not being sufficient to awake the sleeper; whilst, on the other hand, the first stroke is enough to break the repose of him who is impressed with the effectual desire of profiting by the warning. And thus it may happen that, of two persons in the same room, either shall be at once aroused by a sound which

produces no disturbance in the slumbers of the other. To this influence of previous impressions, whether habitual, or but once forcibly made, we are also to refer the spontaneous termination of the state of sleep at particular times, without any sensorial excitement from external impressions. Thus, many persons who are accustomed to rise at a particular hour, wake regularly at that hour, whether they have gone to rest early or late; so that the act of spontaneously awakening is no proof that the desirable amount of repose has been obtained. But what is more remarkable is, that many individuals have the power of determining, at the time of going to rest, the hour at which they shall rise, so as to awake from a profound sleep at the precise time fixed upon. In others, however, the desire to rise at a particular hour only induces a state of restlessness throughout the night, destroying the soundness of the slumbers; the individual awakes many times in the night, with the belief that the hour is past, and very possibly oversleeps it after all, the system being worn out by the need of repose.

535. The *Amount of Sleep* required by man is affected by so many conditions, especially *age*, *temperament*, *habit*, and *previous exhaustion*, that no general rule can be laid down on the subject.—The condition of the *fœtus in utero* may be regarded as one of continual slumber; the apparatus of animal life being completely secluded from all stimuli which could arouse it into activity, whilst the energy of the organic functions is entirely directed to the building-up of the fabric. On its first entrance into the world, the infant continues to pass the greater part of its time in slumber; and this is particularly to be noticed in cases of premature birth, the seven months' child seeming to awake only for the purpose of receiving food, and giving but little heed to external objects, whilst even the eight months' child is considerably less alive to sensory impressions than one born at the full time. The excess of activity of the *constructive* over the *destructive* operations, which characterizes the whole period of infancy, childhood, and adolescence (CHAP. XX.), requires that a larger portion of the diurnal cycle shall be passed in sleep (during which the former may be carried on without hindrance), than is requisite when adult age has been attained, the two sets of changes being then balanced; and the amount of sleep to which the system shows itself disposed, gradually diminishes from three-fourths to one-half, and from one-half to one-third, or even to one-quarter, of the twenty-four hours. It is to be noticed that the sleep of children or young persons is not only longer than that of adults, but is also more profound. On the other hand, as age advances, and the bodily and mental activity of the waking state decreases, a smaller amount of sleep suffices; or, if the slumber be protracted, it is usually less deep and refreshing. It may be noticed, however, that very old persons usually pass a large proportion of their time in sleep, or rather in a sort of heavy doze, especially after meals; as if, in consequence of the want of energy of their nutritive operations, a very long period of repose is necessary to repair the waste which takes place during their short period of activity.—In regard to the influence of *temperament*, it may be remarked that a plethoric habit of body, sustained by full diet, usually predisposes to sleep, provided that the digestive powers be in a vigorous condition; persons of this constitution frequently pass nine or ten hours in slumber, and maintain that they cannot be adequately refreshed by less. On the other hand, thin wiry people, in whom the 'nervous' temperament predominates, usually take comparatively little sleep, notwithstanding the greater activity of their nervous system when they are awake; but their slumber, while it lasts, is generally very deep. Persons of 'lymphatic' temperament, heavy passionless people, who may be said to live very slowly,

are usually great sleepers; but this is rather because, through the dulness of their perceptions, they are less easily kept awake by sensorial or mental excitement, than because they really require a prolonged cessation of activity. As they are half asleep during the waking state, so would it appear that the constructive operations must be far from active while they are asleep, so little do they seem restored by the repose.—The amount of sleep, *cæteris paribus*, required by individuals, is very greatly influenced by *habit;* and, contrary to what we might anticipate, we find that the briefest sleepers have usually been men of the greatest mental activity. Thus Frederick the Great and John Hunter are said to have only required five hours' sleep out of the twenty-four: and General Elliott, celebrated for his defence of Gibraltar, is recorded not to have slept more than four hours out of the twenty-four. It may be doubted whether it would be possible for any one to sustain a life of vigorous exertion upon a smaller allowance than this; and the general fact is, that from six to eight hours of repose, out of every twenty-four, are required to keep the system of an adult in a state of healthful activity. The influence of habit may be brought to bear upon the protraction, as well as on the abbreviation, of the usual period. Thus Quin, the celebrated actor, could slumber for twenty-four hours successively; and Dr. Reid, the metaphysician, could take as much food, and afterwards as much sleep, as were sufficient for two days.—It is needless to dwell upon the obvious fact, that other things being equal, the amount of sleep required by man is proportional to the *amount of mental exertion* put forth during the waking hours; since this is an obvious result of what has been laid down as the cause of the demand for sleep. It may be remarked, however, that we must not measure the *amount* of sleep by its *duration* alone: since its *intensity* is a matter of equal importance. The light slumber which is disturbed by the slightest sounds, cannot be as renovating as the profound sopor of those whom no ordinary noise will awake.

536. There are certain states of the Encephalic centres, in which there is an *entire absence of Sleep;* and this may continue for many days, or even for weeks or months. Insomnia is, for instance, one of the characteristics of acute Mania, and may also exist in various forms of Monomania; it is usually, also, one of the symptoms of incipient meningeal inflammation; and it may constitute a specific disease in itself. In all these cases, however, the preponderance of the *destructive* processes over the *constructive* manifests itself, sooner or later, in the exhaustion of the mental and bodily powers. Thus Mania, when prolonged or frequently recurring, subsides into Dementia; and if it continue for any length of time, is sure to be followed by a great sense of wretchedness and prostration frequently accompanied by continual restlessness. Such effects, too, in a less aggravated degree, result from habitual *deficiency* of sleep; whether this be due to emotional excitement which keeps repose at bay, or to a voluntary determination to keep the intellect in activity. This is a very common occurrence among industrious students, who, with a laudable desire for distinction, allow themselves less than the needed quantum of repose. Headache, tension, heat, throbbing, and various other unpleasant sensations in the head, give warning that the brain is being overtasked; and if this warning be not taken, sleep, which it was at first difficult to resist, becomes even more difficult to obtain; a state of general restlessness and feverish excitement is induced; and if, in spite of this, the effort be continued, serious consequences in the form of cerebral inflammation, apoplexy, paralysis, fever, insanity, or loss of mental power, more or less complete, are nearly certain to be induced. Some individuals can sustain such an effort much longer than others, but it is a great mistake to suppose that they are not

equally injured by it; in fact, being possessed with the belief that they are not suffering from the exertion, they frequently protract it, until a sudden and complete prostration gives a fearful demonstration of the cumulative effects of the injurious course in which they have been persevering. Those, consequently, who are earlier forced to give way, are frequently capable of accomplishing more in the end.—In regard to the degree of *protraction* of sleep which is consistent with a healthy state of the system in other respects, it is difficult to speak with certainty. Of the numerous well-authenticated instances on record,* in which sleep has been continuously prolonged for many days or even weeks, it is enough here to state that they cannot be regarded as examples of natural sleep; the state of such persons being more closely allied to hysteric coma. An unusual tendency to ordinary sleep generally indicates a congested state of the brain, tending to apoplexy; and it has been stated that apoplexy has been actually induced by the experimental attempt to ascertain how large a proportion of the diurnal cycle might be spent in sleep.—Thus, on either side, inattention to the dictates of Nature, in respect to the amount of sleep required for the renovation of the system, becomes a source of disease, and should therefore be carefully avoided.

537. *Dreaming.*—We have hitherto spoken of Sleep in its most complete or profound form; that is, the state of complete unconsciousness. But with the absence of consciousness of external things, there may be a state of mental activity of which we are more or less distinctly cognizant at the time, and of which our subsequent remembrance in the waking state varies greatly in completeness. The chief peculiarity of this state of *dreaming* appears to be, that there is an entire suspension of volitional control over the current of thought, which flows on automatically, sometimes in a uniform coherent order, but more commonly in a strangely incongruous sequence. The former is most likely to occur when the mind simply takes up the train of thought on which it had been engaged during the waking hours, not long previously; and it may even happen that, in consequence of the freedom from distraction resulting from the suspension of external influences, the reasoning processes may thus be carried on during sleep with unusual vigour and success, and the Imagination may develop new and harmonious forms of beauty.† The more general fact is, however, that there is an entire want of any ostensible coherence between the ideas which successively present themselves to the consciousness; and yet we are completely unaware of the incongruousness of the combinations which are thus formed. It has been well remarked that "nothing surprises us in dreams." All probabilities of "time, place, and circumstance" are violated; the dead pass before us as if alive and well; even the sages of antiquity hold personal converse with us; our friends at the Antipodes are brought upon the scene, or we ourselves are conveyed thither, without the least perception of the intervening distance; and occurrences, such as in our waking state would excite the strongest emotions, may be contemplated without the slightest feeling of a painful or pleasurable nature.

* Such, for example, as that of Samuel Chilton ("Phil. Trans.," 1694), and that of Mary Lyall ("Trans. of Roy. Soc. of Edinb.," 1818).

† Thus, Condorcet saw in his dreams the final steps of a difficult calculation which had puzzled him during the day; and Condillac tells us that, when engaged in his "Cours d'Etude," he frequently developed and finished a subject in his dreams, which he had broken off before retiring to rest. Coleridge relates of himself that his fragment "Kubla Khan" was composed during sleep, which had come upon him whilst reading the passage in Purchas's "Pilgrimage," on which the poetical description was founded, and was written down immediately on awaking, "the images rising up before him as things, with a parallel production of the corresponding expressions, without any sensation or consciousness of effort."

Facts and events long since forgotten in the waking state, and remaining only as latent impressions on the Cerebrum, present themselves to the mind of the dreamer; and many instances have occurred in which the subsequent retention of the knowledge thus re-acquired has led to most important results.* But one of the most remarkable of all the peculiarities in the state of dreaming, is the *rapidity* with which trains of thought pass through the mind; for a dream in which a long series of events has seemed to occur, and a multitude of images has been successively raised up, has been often certainly known to have occupied only a few minutes, or even seconds, although whole years may seem to the dreamer to have elapsed. There would not appear, in truth, to be any limit to the amount of thought which may thus pass through the mind of the dreamer, in an interval so brief as to be scarcely capable of measurement; as is obvious from the fact, that a dream involving a long succession of supposed events, has often distinctly originated in a sound which has also awaked the sleeper, so that the whole must have passed during the almost inappreciable period of transition between the previous state of sleep and the full waking consciousness.† Hence it has been argued by some, that *all* our dreams really take place in the momentary passage between the states of sleeping and waking; but such an idea is not consistent with the fact, that the course of a dream may often be traced by observing the successive changes of expression in the countenance of the dreamer. It seems, however, that those dreams are most distinctly remembered in the waking state which have passed through the mind during the transitional phase just alluded to; whilst those which occur in a state allied to Somnambulism are more completely isolated from the ordinary consciousness.—There is a phase of the dreaming state which is worthy of notice as marking another gradation between this and the vigilant state; that, namely, in which the dreamer has a consciousness that he is dreaming, being aware of the unreality of the images which present themselves before his mind. He may even make a voluntary and successful effort to prolong them if agreeable, or to dissipate them if unpleasing; thus evincing the possession of a certain degree of that directing power, the entire want of which is the characteristic of the true state of Dreaming.

538. But the sensibility to external impressions may not be entirely suspended in Dreaming; and it is curious that even where sensations are not recognized by the mind of the dreamer as proceeding from external objects, they may affect the course of its own thoughts; so that the character of the dreams may be in some degree predetermined by such an arrangement of sensory impressions as is likely to modify them. This is especially the case in regard to the dreamy state induced by certain narcotics, such as the Hachisch (a preparation of *Cannabis Indica*), employed for this purpose in the East; for the emotional condition of the individual under its influence is entirely under the control of external impressions; so that those who give themselves up to the intoxication of the *fantasia*, take care to withdraw themselves from everything that could give their delirium a tendency to melancholy, or excite in them anything else than feelings of pleasurable enjoyment.‡

* See a number of such cases in Dr. Abercrombie's "Inquiries concerning the Intellectual Powers."

† The only phase of the waking state, in which any such intensely rapid succession of thoughts presents itself, is that which is now well attested as a frequent occurrence, under circumstances in which there is imminent danger of death, especially by drowning; the whole previous life of the individual seeming to be presented instantaneously to his view, with its every important incident vividly impressed on his consciousness, just as if all were combined in a picture, the whole of which could be taken in at a glance.

‡ See the Author's article, "Sleep," in the "Cyclop. of Anat. and Phys.", vol. iv. pp. 688–690; and Moreau, "Du Hachisch et de l'Aliénation Mentale, Etudes Psychologiques," p. 67.

Moreover, there are certain forms of ordinary Dreaming in which the whole succession of thought and feeling (which is made manifest by the words occasionally uttered, or by the play of countenance, or by the more active movements of the dreamer) may be governed by external suggestion; as, for example, in the well-known case of the officer who amused his friends by acting his dreams during the expedition to Louisburgh, the course of these dreams being capable of direction by whispering into the sleeper's ear, especially if this was done by a friend with whose voice he was familiar.* Such forms of Dreaming constitute a transition to the state of Somnambulism.

539. *Somnambulism.*—The phenomena of Somnambulism are so various, that it is difficult to give any general definition that shall include the whole; but it is a condition which is common to all forms of this state, that the controlling power of the Will over the current of thought is entirely suspended, and that all the actions are directly prompted by the ideas which possess the mind; and the differences chiefly arise out of the mode in which the succession of ideas is directed, this being in some cases a coherent sequence through the whole of which some one dominant impression may be traced, whilst in other instances it is more or less completely determinable by external suggestions. These two forms are thus parallel to the states of spontaneous Abstraction and artificial Reverie (Electro-Biology) respectively; but differ from them both in this essential feature—that they occur in a state of consciousness so far distinct from the ordinary waking condition, as not to be connected with it by the ordinary link of Memory; and that although the course of thought in Somnambulism usually manifests the directing influence of previous habits, and the knowledge of persons and things possessed during the waking state may be readily brought before the mind, yet nothing which occurs during the state of Somnambulism is ever retraced spontaneously, or can be brought back by an act of recollection. Impressions upon the nervous system, however, are sometimes left by strong emotional excitement, which give rise to subsequent feelings of discomfort, of whose origin the individual is entirely unconscious.† —In the first of the phases just referred to, a train of reasoning is often carried out with remarkable clearness and correctness, and its results expressed in appropriate language, or otherwise acted on. Thus, a mathematician may work out a difficult problem, an orator may make a speech appropriate to the occasion on which he supposes himself to be called up, or an author may compose and commit to writing poetry or prose upon the subject which occupies his thoughts. But it is a frequent defect of the intellectual operations carried on in this condition, that through the complete absorption of the attention by one set of considerations, no account is taken of others which ought to modify the conclusion; and this, although it may be palpably inconsistent with the teachings of ordinary experience, is not felt to be so, unless the latter should happen to present themselves unbidden to the thoughts.

540. The second of the phases above-mentioned, which is especially seen in the *artificial* Somnambulism induced by the (so-called) *Mesmeric* process, or by the fixed gaze at a near object (as practised by Mr. Braid under the name of *Hypnotism*), is essentially the same as that of the "biological" condition, save in the different relation which they respectively bear to the waking state; for there is the same readiness to receive new impressions through the senses (the visual

* This case is detailed by Dr. Abercrombie ("Inquiries concerning the Intellectual Powers," 5th ed., p. 277), on the authority of Dr. Gregory, to whom it was related by a gentleman who witnessed it. A case of a very similar nature, the subject of which was a medical student at Edinburgh, is related in Smellie's "Philosophy of Natural History."

† See a very curious example of this kind, which fell under the Author's own observation, narrated in the article "Sleep," in the "Cyclop. of Anat. and Phys.," vol. iv. p. 693.

sense, however, being generally in abeyance), and the same want of persistence in any one train of ideas, the direction of the thoughts being entirely determined by the suggestions which are introduced from without. In either of these extreme forms of Somnambulism, and in the numerous intermediate phases which connect the two, the consciousness seems entirely given up to the one impression which is operating upon it at the time; so that whilst the attention is exclusively directed upon any object, whether actually perceived through the senses, or brought suggestively before the mind by previous ideas, nothing else is felt. Thus there may be complete insensibility to bodily pain, the somnambulist's whole attention being given to what is passing in his mind; yet in an instant, by directing the attention to the organs of sense, the anæsthesia may be replaced by ordinary sensibility; or, by the fixation of the attention on any one class of sensations, these shall be perceived with most extraordinary acuteness, whilst there may be a state of complete insensibility as regards the rest.—Thus, the Author has witnessed a case in which such an exaltation of the sense of Smell was manifested, that the subject of it discovered without difficulty the owner of a glove placed in his hand, in an assembly of fifty or sixty persons; and in the same case, as in many others, there was a similar exaltation of the sense of Temperature. The exaltation of the Muscular Sense, by which various actions that ordinarily require the guidance of vision, are directed independently of it, is a phenomenon common to the "mesmeric" with various other forms of artificial as well as of natural Somnambulism. The Author has repeatedly seen Mr. Braid's "hypnotized" subjects write with the most perfect regularity, when an opaque screen was interposed between their eyes and the paper, the lines being equidistant and parallel; and it is not uncommon for the writer to carry back his pen or pencil to dot an *i* or cross a *t*, or make some other correction in a letter or word. Mr. Braid had one patient who would thus go back and correct with accuracy the writing on a whole page of note-paper; but if the paper was moved from the position it had previously occupied on the table, all the corrections were on the *wrong* points of the paper as regarded the *actual* place of the writing, though on the *right* points as regarded its *previous* place; sometimes, however, he would take a fresh departure, by feeling for the upper left-hand corner of the paper, and all his corrections were then made in their right positions, notwithstanding the displacement of the paper.—So, again, when the attention of the somnambulist is fixed upon a certain train of thought, whatever may be spoken in harmony with this is heard and appreciated; but what has no relation to it, or is in discordance with it, is entirely disregarded.*

541. It is among the most curious of the numerous facts which Mr. Braid's investigations upon artificial Somnambulism have brought to light, that the suggestions derived from the "muscular sense" have a peculiar potency in determining the current of thought. For if the face, body or limbs, be brought into an attitude that is expressive of any particular emotion, or that corresponds with that in which it would be placed for the performance of any voluntary action, the corresponding mental state—that is, either an Emotional condition affecting the general direction of the thoughts, or the Idea of a particular action—is called up in respondence to it. Thus, if the hand be placed upon the vertex, the Somnambulist will frequently, of his own accord, draw his body up to its fullest height, and throw his head slightly back; his countenance then assumes an expression of the most lofty pride, and the whole train of thought is obviously under the domination of this feeling; as is manifested by the replies which the individual makes to interrogatories, and by the

* For a further discussion of this subject see the Author's "Mental Physiology and Nature."

tone and manner in which these are delivered. Where the first action does not of itself call forth the rest, it is sufficient to straighten the legs and spine, and to throw the head somewhat back, to arouse the emotion, with its corresponding manifestation, in its full intensity. If, during the most complete domination of this emotion, the head be bent forwards and the body and limbs be gently flexed, the most profound humility then takes place. So, again, if the angles of the mouth be gently separated from one another, as in laughter, a hilarious disposition is immediately generated; and this may be made to give place to moroseness, by drawing the eyebrows towards each other and downwards upon the nose, as in frowning.* So, again, if the hand be raised above the head, and the fingers be flexed upon the palm, the idea of climbing, swinging, or pulling at a rope is called up in such as have been used to such kinds of exertion; if, on the other hand, the fingers be flexed when the arm is hanging down at the side, the idea suggested is that of lifting a weight; and if the same flexure be made when the arm is advanced forwards in the position of striking a blow, the idea of fighting is at once aroused, and the Somnambulist is very apt to put it into immediate execution.†

CHAPTER XIV.

OF THE ORGANS OF THE SENSES, AND THEIR FUNCTIONS.

1. *Of Sensibility in General.*

542. We have seen that the conscious Mind is affected by impressions made upon the corporeal organism—or, in other words, that Sensation is produced—through the instrumentality of a certain part of the Encephalon termed the *Sensorium*, which is the general centre of the nerves both of "special" and of "common" sensibility: the former connect it with the special Organs of Sense, the latter with the body generally, to the several parts of which they are by no means uniformly distributed, some tissues being altogether destitute of them. Those parts of the body which are endowed with sensory fibres, and impressions on which, therefore, give rise to sensation, are ordinarily spoken of as *sensitive;* and different parts are said to be sensitive in different degrees, according to the strength of the sensation produced by a corresponding impression on each. In accordance with the general fact of the dependence of all Nervous action on the continuance of the Circulation of the blood, it is found that the sensory nerves are distributed pretty much in the same proportion as the blood-vessels: that is to say, in the non-vascular tissues—such as the epidermis, hair, nails, cartilage, and bony substance of the teeth—no nerves

* The Author has not only repeatedly witnessed all these effects, as produced by Mr. Braid upon "hypnotized" subjects, of whom several had never been previously in that condition, and had no idea whatever of what was expected from them; but he has been assured by a most intelligent medical friend, who has paid special attention to the psychological part of this inquiry, that having subjected himself to Mr. Braid's practice, and having been only partially thrown into the "hypnotic" state, he distinctly remembers everything that was done, and can retrace the uncontrollable effect upon his emotional state, which was produced by this management of his muscular apparatus.

† On one occasion on which the Author witnessed this result, a violent blow was struck, which chanced to alight upon a second somnambulist within reach; *his* combativeness being thereby excited, the two closed, and began to belabour one another with such energy, that they were with difficulty separated. Although their passions were at the moment so strongly excited, that even when separated they continued to utter furious denunciations against each other, yet a little discreet manipulation of their muscles soon calmed them and restored them to perfect good-humour.

exist, and there is an entire absence of sensibility; and in those whose vascularity is trifling, as in the case with bones, tendons, ligaments, fibrous membranes, and other parts whose functions are simply mechanical, and even with serous and areolar membranes, there are few nerves, and the sensibility is dull. Many of these textures are acutely sensible, however, under certain circumstances; thus, although tendons and ligaments may be wounded, burned, &c., without much consciousness of the injury being aroused, they cannot be stretched without the production of considerable pain; and the fibrous, serous, and areolar tissues, when their vascularity is increased by inflammation, also become extremely susceptible of painful impressions. All very vascular parts, however, do not possess acute sensibility; the muscles, for instance, are furnished with a large supply of blood, to enable them to perform their peculiar function; but they are not sensitive in by any means the same proportion. Even the substance of the brain, and of the nerves of special sensation, appears to be destitute of this endowment; and the same may be said of the mucous membranes lining the interior of the several viscera, which, in the ordinary condition, are much less sensitive than the membranes that cover those viscera, although so plentifully supplied with blood for their especial purposes. The most sensitive of all parts of the body is the Skin, in which the sensory nerves spread themselves out into a minute network; and even of this tissue, the sensibility differs greatly in different parts (§ 548).—The organs of *Special* Sensation become, by the peculiar character of the nerves with which they are supplied, the recipients of impressions of a particular kind: thus, the Eye is sensible to light, the Ear to sound, &c.; and whatever amount of *ordinary* sensibility they possess, is dependent upon other sensory nerves. The eye, for example, contrary to the usual notions, is a very insensible part of the body, unless affected with inflammation; for though the mucous membrane which covers its surface, and which is prolonged from the skin, is acutely sensible to tactile impressions, the interior, with the exception of the Iris, is by no means so, as is well known to those who have operated much on this organ. And the common sensory nerves which supply certain parts of the body, are adapted to receive and convey to the mind impressions of particular kinds, with much greater readiness than they communicate those of a different description; thus the sensibility to tickling is much greater on some parts of the surface than on others; and this kind of excitement, applied to the genitals or to the nipple, produces sensations of a most peculiar order.

543. An active Capillary Circulation being essential to the sensibility of every part supplied with nerves, any cause which retards this deadens the sensibility, as is well seen with regard to Cold; and, on the other hand, an increase in its activity produces a corresponding increase in the sensibility, as is peculiarly evident in the "active congestion" which usually precedes and accompanies Inflammation. A diminution or increase of sensibility to external impressions may arise, however, not only from an abnormal state of the circulation in the organ or part itself, but from the similar conditions affecting that part of the Sensorium in which the impressions are received. Thus in those various conditions of the Encephalon, in which either a stagnation of the circulation, or an abnormal state of the blood (such as that produced by anæsthetic agents), occasions a diminished functional activity in the Sensorial centres, this is marked by obtuseness to sensory impressions; on the other hand, in active congestion of the brain, the most ordinary external impressions produce sensations of an unbearable violence; and in that peculiar condition of the nervous system known under the name of Hysteria, the patients often manifest the same hyperæsthesia, even when the circulation is in a feeble,

rather than in an excited state.* It is remarkable that the sensibility of the mucous membranes lining the internal organs is less exalted by the state of inflammation than is that of most other parts; and in this arrangement we may trace a wise and beneficent provision; since, were it otherwise, the functions necessary to life could not be performed without extreme distress, whenever a very moderate amount of disorder might exist in the viscera. If a joint is inflamed we can give it rest; but to the actions of the alimentary canal we can give little voluntary respite.

544. It is through the medium of Sensation that we acquire a knowledge of the material Universe around us, by the psychical operations which its changes excite in ourselves. The various kinds or modes of Sensation *suggest* to us various ideas regarding the properties of matter; and these properties are known to us, only through the changes which they produce in the several organs. It is well known that instances occur, in which, from some imperfection of the organization, there is an incapacity for distinguishing colours or musical tones, whilst there is no want of sensibility to light or sound; and that some persons are naturally endowed with a much greater range of the sensory faculties than that possessed by others. Hence it does not seem at all improbable, that there are properties of matter of which none of *our* senses can take immediate cognizance; and which other beings might be formed to perceive, in the same manner as *we* are sensible to light, sound, &c. Thus, many animals are affected by atmospheric changes in such a manner that their actions are regarded by Man as indications of the probable state of the weather; and the same is the case in a less degree with some of our own species, who are peculiarly susceptible of the like influences.—Now the most universal of all the qualities or properties of Matter, on which, in fact, our notion of it is chiefly founded, is its occupation of space, producing a more or less complete *resistance* to displacement; and this quality is that through which alone any knowledge of the external world can be obtained by a large proportion of the lower Animals; *contact* between their own surface and some material body being required to produce sensation. We shall presently see, however, that the idea of the *shape* of a body which we form from the touch, results from a very complex process, such as animals of the lower grades can scarcely be supposed to exercise. There can be little doubt that, next to resistance sensibility to *temperature* is the most universally diffused through the Animal kingdom; and probably the consciousness of *luminosity* is the next in the extent of its diffusion.† It is probable that the sense of *taste* (which has a close affinity to that of touch) exists very low down in the animal scale, being obviously of great importance in the selection of food; but the Anatomist has no means of ascertaining where this refinement exists, and where it does not; since the organs of taste and touch are very similar. The sense of *hearing* does not seem to be distinctly present among Invertebrate animals, except in such as approach most nearly to the Vertebrata; it is not improbable, however, that sonorous vibrations may produce an effect upon the system of those animals which do not receive them as *sound*. The

* The influence of toxic agents introduced into the blood, in producing Anæsthesia and Hyperæsthesia, constitutes a very wide field of inquiry, the investigation of which has been ably commenced by Dr. Anstie, in his interesting work on Stimulants and Narcotics (London, 1864). It is remarkable that *Lead* and *Alcohol* should be capable of inducing either of these states.

† There is good reason to believe, from observation of their habits, that many animals are susceptible of the influence, and are directed by the guidance, of *light*, whose organs are not adapted to receive true visual impressions, or to form optical images; and such would seem to be the function of the red spots, frequently seen on prominent parts of the lower Arthropoda and Mollusca, and even of some Echinodermata. Wherever these are of sufficient size to allow their structure to be examined, they are found to be largely supplied with nerves, but to be destitute of the peculiar organization which alone constitutes a true *eye*.

sense of *smell*, which is concerned with one of the least general properties of matter, appears to be the least widely diffused among the whole; being only possessed in any high degree by Vertebrate animals, and being but feebly present in a large proportion of these.

545. Besides the various kinds of sensibility which have been just enumerated, there are others which are ordinarily associated together, along with the sense of material resistance (and its several modifications), and the sense of temperature, under the head of Common Sensation; but several of them, especially those which originate in the body itself, can scarcely be regarded in this light. Such are the feelings of hunger and thirst; that of nausea; that of distress resulting from suspended aeration of the blood; that of "sinking at the stomach," as it is vulgarly but expressively described, which results from strong mental emotion; the sexual sense, and perhaps some others.—Now, in regard to all these, it is impossible in the present state of our knowledge to say, whether their peculiarity results from the particular constitution of the nerves that receive and convey them, or only from a modification of the impressing causes, from the particular endowments of their ganglionic centres, and from the mode in which they operate. Thus we have no evidence whether the nervous fibrils which convey from the lungs the sense of distress resulting from deficient aeration, are of the same or of a different character from those which convey from the surface of the air-passages the sense of the contact of a foreign body. But as we know that all the trunks along which these peculiar impressions travel, do minister to ordinary sensation, whilst the nerves of truly "special" sensation are not sensible to tactile impressions, it is evident that the probability seems in favour of the identity of the fibres which minister to these sensations with those of the usual sensory character. We shall see that with regard to the sense of Temperature there is strong evidence that its peculiarity partly depends on the speciality of the apparatus by which impressions are received at the peripheral extremities of the tactile nerves, and partly upon some peculiarity in the transmitting fibres.

546. There are certain external agencies which can excite changes in the Sensorium through several different channels; the sensation being in each case characteristic of the particular nerve on which the impression is made. Thus pressure, which produces through the nerves of common sensation the feeling of resistance, is well known to occasion, when exerted on the eye, the sensation of light and colours; and, when made with some violence on the ear, to produce "tinnitus aurium." It is not so easy to excite sensations of taste and smell by mechanical irritation; and yet, as was shown by Dr. Baly,* this may readily be accomplished in regard to the former. The sense of nausea may be easily produced, as is familiarly known, by mechanical irritation of the fauces. Electricity still more completely possesses the power of affecting all the sensory nerves with the changes which are peculiar to them; for, by proper management, an individual may be made conscious at the same time of flashes of light, of distinct sounds, of phosphoric odour, of a peculiar taste, and of pricking sensations, all excited by the same cause, the effects of which are modified by the respective peculiarities of the instruments through which it operates.—But although there are some stimuli which can produce sensory impressions on all the nerves of sensation, it will be found that those to which any one organ is *peculiarly* fitted to respond, produce little or no effect on the rest. Thus the ear cannot distinguish the slightest difference between a luminous and a dark object. A tuning-fork which, when laid upon the ear whilst vibrating, produces a distinct musical tone, excites no other sensation when placed upon the eye than a slight jarring feeling. The most delicate

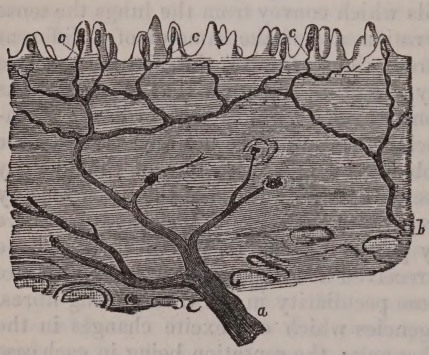
* Translation of Müller's "Elements of Physiology," p. 1062, *note*.

touch cannot distinguish a substance which is sweet to the taste from one which is bitter; nor can the taste (if the communication between the mouth and the nose be cut off) perceive anything peculiar in the most strongly odoriferous bodies.—It may hence be inferred that no nerve of *special* sensation can, by any possibility, take on the function of another.*

2. *Sense of Touch.*

547. By the sense of Touch, as commonly understood, is meant that modification of the common sensibility of the body, of which the Cutaneous surface is the special seat, and by means of which sensations of pressure and temperature are perceived. The Skin is peculiarly adapted for this purpose, not merely by the large amount of sensory nervous fibres which are distributed in its substance, but also by its possession of a papillary apparatus in which these nerves for the most part terminate, or rather commence. The *papillæ* are little elevations of the surface of the cutis, usually simply-conical or clavate in form (Fig. 249), but sometimes presenting several summits. They are divisible into three kinds: first, those which are exclusively vascular, and which constitute the immense majority; secondly, those which are both vascular and nervous; and thirdly, those which are exclusively nervous and are extremely limited in number. On the head, neck, trunk, and greater part of the limbs, there are on the average about 100 papillæ to the square millimeter, and as the body presents a surface of about 15,000 square centimeters, the total number of papillæ is about 150 millions.† On the palmar surface of the hand they are arranged in rows, and are there much less numerous (about 36 being present in each square millimeter). The papillæ are particularly numerous, though without any definite arrangement, on the red surface of the lips, on the penis of the male, on the labia minora and clitoris of the female, and on the nipples of both sexes. Their size is in inverse relation to their number. The nerves of the skin form a plexus near the surface of the corium just beneath the epithelium, and from this plexus fine fibrils come off, which entering the rete Malpighii ascend towards the *stratum corneum*, communicating with each other in the rete Malpighii, to form what Klein regards as a terminal network.‡ Mojsisovics has, however, observed in the pig free club-shaped extremities between the cells of the Malpighian layer. Each sensory papilla receives one or more nerve-fibres from the plexus

Fig. 249.



Vertical Section of the *Skin* of the palmar surface of the fore-finger, showing the branches of cutaneous nerves, *a*, *b*, inosculating to form a terminal plexus, of which the ultimate ramifications pass into the cutaneous papillæ, *c*, *c*, *c*.

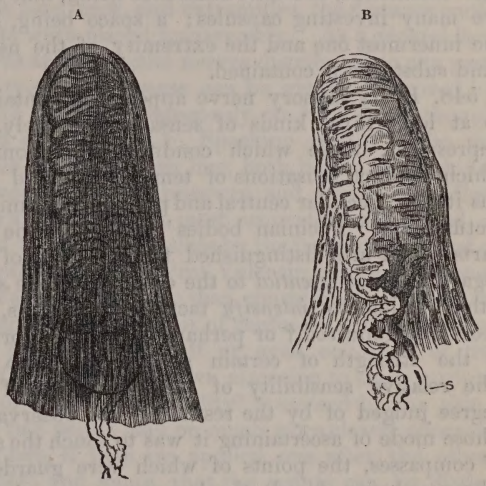
* It does not, however, seem a thing altogether incredible, that impressions powerfully arousing one sense may consentaneously excite another sense, and in evidence of this Nussbaumer, "Monatsschrift f. Ohrenheilkunde," March, 1873, records the fact, that both he and his brother can perceive certain colours when the auditory nerve is powerfully excited by certain sounds. In one brother "A" on the piano produces the subjective impression of dark Prussian blue, in the other brother it produces dark yellow. Some of the colours, though differing in the two brothers, are not produced by any sound.

† Sappey, "Anatomie Descriptive," 1872, t. iii. p. 535.

‡ "Centralblatt f. d. Med. Wiss.," 1877, p. 289.

which is formed by the inosculation of the ramifications of the cutaneous nerves (Fig. 249); and these nerve-fibres seem to terminate (at least in the papillæ of the palm of the hand and of the lips, and in the simple papillæ of the tongue) in a peculiar "axile body," which occupies the principal part of the interior of the papilla (Fig. 250).* The *tactile corpuscles* are specially modified terminations of one or more medullated nerve fibres. According to Izquierdo† they consist of a homogeneous dark external layer, surrounding an internal and more transparent mass of protoplasm. The nerves run without division sometimes only as far as the lower pole, sometimes as far as the middle, and sometimes even to the extremity of the corpuscle, frequently winding around it once or twice, and constricting it at these points. The sheath of Schwann then becomes continuous with the outer layer of the corpuscle, whilst the axis-cylinder penetrates and fuses with the central mass of protoplasm. The outer surface of the corpuscles presents numerous transverse cells (Fig. 250 B), the nuclei of which are oblong. After section of the uterus the tactile papillæ undergo fatty degeneration. A very simple form of the axile bodies has been described by Krause as occassionally occuring in the conjunctiva, lips, and soft palate, in the tongue, and in the glans penis and glans clitoridis.‡

FIG. 250.



Tactile Papillæ of Meissner, from the Skin of the palmar surface of the fore-finger, showing the *tactile corpuscles* or 'axile bodies':—A, in a natural state; B, treated with acetic acid.

* For details in regard to the structure of the corpuscula tactûs and the terminations of the tactile nerves, see Prof. Wagner in the Göttingen "Gelehrte Nachrichten" for Feb. 1852, and Müller's "Archiv," 1852, Heft 4; Prof. Kölliker in "Zeitsch. für wissensch. Zool.," June, 1852, and in his "Mik. Anat.," Band ii. p. 24. Dalzell, in "Edin. Monthly Journal," March, 1853; Ecker, "Icon. Physiol.," plate xvii.; Leydig, Müller's "Archiv," 1856, p. 50, and Schultze's "Archiv. f. Mic. Anat.," 1868, p. 195; Gerlach, "Mikroskop. Studien," Erlangen, 1858; Krause, "Die Terminal Körperchen der einfach Sensibeln Nerven," Hanover, 1860; Huxley, in "Cyclop. of Anat. Physiol.," Suppl., Art. "Tegument. Organs," 1859, p. 503; Meissner, "Beiträge," plate i. figs. 6 and 8; Henle, "Handb. der System. Anat.," 1862, Band ii. p. 13; Fick, "Lehrb. der Anat. der Sinnes-organe," 1862, p. 22; Tomsa, "Wien. Med. Wochens.," 1865, Band xv. p. 53; Rouget, "Archiv. de Physiol.," 1868, p. 598; Michelson, "Centralblatt," 1869, p. 446; G. Ciaccio, Moleschott's "Untersuch.," Band x. p. 579; J. Schöbl, Schultze's "Archiv," Band vii. p. 260, and viii. p. 295; Th. Eimer, Idem, Band vii. p. 181; L. Stieda, Idem, Band viii. p. 274; W. Beil, Abst. in "Centralblatt," 1872, p. 692; Sertoli, Abst. in "Centralblatt," 1872, p. 692; Budge, "Centralblatt," 1873, p. 594; Langerhans, Schultze's "Archiv," Band ix. p. 730; Jobert, "Comptes Rendus," 1874, p. 820; G. Thin, "Journ. of Anat. and Phys.," 1874, p. 30; Biesiadecki, in Stricker's "Hum. and Comp. Histology," vol. ii. p. 232; Grandry, "Journal de l'Anatomie," t. vi. 1870, p. 390. References to all the more recent literature will be found in Klein and Noble's beautifully executed "Atlas of Histology," 1880, and in Otto Fauke's article, "Tastsinn," in Hermann's "Handbuch der Physiologie," 1880, vol. iii., p. 289.

† "Archiv für Mic. Anat.," Band xvi. p. 367.

‡ Dr. Beale appears to doubt the termination in any instance of sensory nerves by free

Here the nerve forms a "terminal button or knob," consisting of a delicate sheath dotted with nuclei and filled with granular plasma, into which the axis cylinder of the nerve enters terminating by a simple blunt extremity. In the Pacinian bodies, the number of which in Man is estimated by Rauber to be 2142,* a more complex structure is met with than in either of those just mentioned, the chief difference being, that instead of a single sheath there are many investing capsules; a space being, however, always left between the innermost one and the extremity of the nerve, in which a fluid or semi-fluid substance is contained.

548. Every sensory nerve appears to contain afferent fibres that minister to at least three kinds of sensations, namely, those which conduct tactile impressions, those which conduct impressions of pain, and lastly, those which conduct sensations of temperature, and it is not improbable that each has its own peculiar central and peripheral terminal organs. As the "corpuscula tactûs" and "Pacinian bodies" are only to be found in the papillæ of those parts which are distinguished for acuteness of tactile sensibility, we cannot regard them as *essential* to the exercise of the sense of touch; their function, either being to *intensify* tactile impressions, where delicacy of touch is peculiarly required,† or perhaps to supply information in regard to variations in the strength of certain stimuli, as those of temperature or pressure. The relative sensibility of different parts of the Skin may be in some degree judged of by the results of the observations of Prof. E. H. Weber;‡ whose mode of ascertaining it was to touch the surface with the legs of a pair of compasses, the points of which were guarded with pieces of cork; then, (the eyes being closed) the legs were approximated, until they were brought within the smallest distance at which they could be felt to be distinct from one another, which has been termed by Dr. Graves "the limit of confusion." —The following are some of the measurements taken:—

Point of tongue	½ of a line.	Mucous membrane of gums	9 lines.
Palmar surface of third phalanx	1 line.	Lower part of forehead	10 „
Red surface of lips	2 lines.	Lower part of occiput	12 „
Palmar surface of second phalanx	2 lines.	Back of hand	14 „
Palmar surface of metacarpus	3 „	Vertex	15 „
Tip of the nose	3 „	Skin over patella	16 „
Dorsum and edge of tongue	4 „	——— sacrum	18 „
Part of lips covered by skin	4 „	——— acromion	18 „
Palm of hand	5 „	Dorsum of foot	18 „
Skin of cheek	5 „	Skin over sternum	20 „
Extremity of great toe	5 „	Skin beneath occiput	24 „
Hard palate	6 „	Skin over spine, on back	30 „
Dorsum of hand	8 „	Middle of the thigh	30 „

extremities; for he has everywhere obtained demonstrative evidence of a network, the fibres being often of extraordinary tenuity. He believes that in the papillæ of the Skin, and even in the Pacinian bodies, after becoming connected with nuclei or corpuscles the nerve-fibres turn or loop back to the cell from whence they originate.

* "Untersuch.", München, 1867.

† In proof of which, various ingenious experiments have been made by Krause (see "Zeitschrift für Rat. Med.," xvii. p. 278). He explains their presence in the mesentery of the Cat as connected with the mechanism and arrangement of the viscera required for the act of springing.

‡ For similar experiments performed by Dr. Ballard, see "Lancet," 1862, vol. i. p. 303. Dr. Ballard found that in the hand the tip of the index finger was the most, the dorsal surface of the base of the fifth metacarpal bone the least, sensitive part; the limit of confusion in the former being 0·35 of a line, in the latter 5 lines.

It is curious that the distance between the legs of the compasses, as well as the rapidity of their motion when they were lightly drawn over the skin, seemed to be greater (although really less), when it was felt by the more sensitive parts, than when it was estimated by parts of less distinct sensibility. With the extremities of the fingers and the point of the tongue, the distance could be distinguished more easily in the longitudinal direction; on the dorsum of the tongue, the face, neck, and extremities, the distance could be estimated best when the points were placed transversely. As a general fact, it seems that the more numerous are the tactile nerves distributed to any part, the more acute is the sensibility, and the sense can be greatly improved by exercise, the improvement taking place simultaneously on both sides, though only one side may be practised or educated.* Speaking generally also the sensibility of the trunk is greater on the median line, both before and behind, and less at the sides. Differences in the temperature and weight of bodies, were, according to Prof. Weber's observations, most accurately recognized at the parts which were determined to be most sensible by the foregoing method of inquiry.†—It has been since found, however, by Prof. Valentin, who has followed up and extended Prof. Weber's observations, that considerable amount of individual variation exists in regard to the "limit of confusion;" some persons being able to distinguish the points at one-half or even one-third of the distances required by others. Czermak‡ has drawn attention to many curious facts in relation to the "sense of space" or "locality" possessed by the skin; and has particularly shown that two points may be much more closely approximated, and yet distinguished as two, if they are applied one after the other, than if they are applied together; and again, that the points can be distinguished as two, at a shorter distance when gradually approximated from a considerable interval, than if they are gradually separated from an inappreciable interval. If one of the points be much colder than the other, the distance at which they can be distinguished is reduced, but their relative position cannot be accurately estimated. Moistening the skin with an indifferent fluid augments its sensibility. The delicacy of the sense of touch is diminished if the skin be either artificially or naturally stretched; hence the skin of the belly is less sensitive during pregnancy than under ordinary circumstances, and this may also in some measure serve to explain the diminution in sensibility which occurs in the passage from childhood to adult age, though the difference is no doubt partially due to the increased thickness of the epithelium. The theory of the sense of touch which has been suggested by Fick, is that each nerve-fibril breaks up into a pencil of fine filaments at the periphery, which are distributed over a certain space, perhaps on the average about 1-25th of an inch in diameter. An impression made upon any one of these filaments conveys the same sensation to the sensorium, providing no other nerve be distributed to the same space; but this hardly ever occurs, and hence compound sensations arise, by which our perception of the precise spot of the skin touched by a point is accurately determined. Thus, if we suppose the distribution of nerves to be represented by the circles, A, B, C, (Fig. 251) single sensations

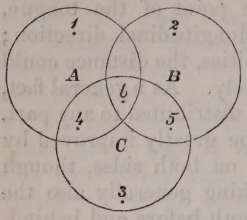
* See Klug in Du Bois-Reymond's "Archiv. f. Physiologie," Jahrg. 1877, p. 275.

† See his Memoir "De Pulsu, Respiratione, Auditu, et Tactu," Lipsiæ, 1834. See also "Récherches sur la Distribution de l'Organe du Sens Tactile," by M. H. Belfield-Lefèvre, Paris, 1837; and Prof. Valentin's "Lehrbuch der Physiologie des Menschen," Band ii. 566. —In the Author's article "Touch" in the "Cyclopædia of Anatomy and Physiology," vol. iv. p. 1169, will be found a Table including the whole series of observations made by Profs. Weber and Valentin, the maxima and minima of the latter being stated, as well as the means.

‡ "Sitz.-ber. der Wiener Akad.," Band xvii. p. 563, Band xxiv. p. 231; and Moleschott's "Untersuch.," Band i. p. 188.

would be produced if a point were applied at 1, 2, or 3, but a compound sensation would be produced if contact were made at 4 or 5, for the fibrils of two nerves, A and C, or B and C, would be implicated; whilst if the impression were made at 6, a still more complex sensation would arise, for then the peripheral branches of three of these nerves would be affected; in all instances a difference in the character of the impression capable of recognition by the mind being produced. It is obvious that the closer these "sensory circles" are, and the more intimately the branches of different nerves are intercalated with one another, the greater will be the accuracy of the sense of locality of that part, or, in other words, the greater will be the facility with which minute differences in the precise spot touched will be appreciated. The experiments of Dr. Paulus* show that the sensitiveness of the skin of the lower extremity, in accordance with a theory propounded by Vierordt, increases with its distance from the axis of rotation of the limb, or, in other words, from the proximal joint, and with the freedom with which its movements can be executed. The leg is thus more sensitive than the thigh, the foot than the leg, and the toes than the foot, the sensitiveness in each division again augmenting from its own proximal joint, except in the single case of the leg proper, where the minimum acuteness is opposite the centre of the tibia; but this, as Paulus points out, really favours Vierordt's theory, since, under different circumstances, sometimes the upper and sometimes the lower part of the leg moves through the greatest arc. In the arm the increase of sensitiveness from the shoulder to the tips of the fingers is as 1 : 24; in the legs as 1 : 8½, which may be accounted for by the greater rapidity required in the movements of the arm as compared with those of the leg. Tactile sensibility is diminished by cold, anæmia, congestion (as by venous compression), long and frequent experimentation (probably owing to exhaustion) and by narcotics, as Atropin, Daturin and Morphia, and by Strychnin and Alcohol.*

Fig. 251.



549. As already stated (§ 544), the ideas communicated to our minds by the sense of Touch, when exercised in its simplest form, are those of *Resistance* and *Temperature*, and it is by the various degrees of resistance which the sensory surface encounters, of which we partly judge by the muscular sense, that we estimate the hardness or softness of the body against which we press. It is only when either the sensory surface or the substance touched is made to change its place in regard to the other, that we obtain the additional notion of *extension* or *space:* this also being derived from the combination of the muscular with the tactile sense. By the impression made upon the papillæ, during the movement of the tactile organ over the body which is being examined, the roughness, smoothness, or other peculiar *characters of the surface* of the latter are estimated. Our knowledge of *form*, however, is a very complex process, requiring not merely the exercise of the sense of touch, but also great attention to the muscular sensations.—It is chiefly, as formerly remarked, in the *variety* of movements of which the hand of Man is capable, that it is superior to that of any other animal; and it cannot be doubted that the sense of Touch thus employed, affords us a very important means of acquiring information in regard to the external world, and especially of correcting many vague and fallacious notions which we should derive from the

* Paulus, "Zeitschrift f. Biologie," Band vii. p. 237; see also Kottenkamp and Ullrich, idem, Band vi. p. 37; and Klug, Op. cit.

† Landois, "Lehrbuch der Physiologie," 1880, p. 883.

sense of Sight, if used alone. On the other hand, it must be confessed that our knowledge would have a very limited range if this sense were the only medium through which we could acquire ideas. It is probably on the sensations communicated through the Touch that the idea of the material world, as something external to ourselves, chiefly rests; but this idea is by no means a logical deduction from our experience of these sensations, being rather an instinctive or intuitive perception directly excited by them.

550. Various experimenters* have endeavoured to determine the accuracy with which the Skin can appreciate impressions of weight or pressure when unassisted by the "muscular sense," that is, when the part experimented on is well supported, as when the hand is laid upon a table, and Eulenburg has constructed a Baræsthesometer, with which pressure can be applied by means of a spring. Eulenburg found that the brow, lips, dorsum of the tongue, cheeks and temples could appreciate a difference of from 1-48th to 1-30th of a given weight (200 : 205—300 : 310 gramme). The dorsal side of the last phalanx of the fingers of the fore-arm and of the hand, the palmar surface of the hand, and the front surface of the fore and upper arm recognized differences of pressure amounting to from 1-10th to 1-20th of the weight applied. The foot and the outer surface of the thighs were much less sensitive. Aubert and Kammler found that on the face and dorsal surface of the upper extremity, the pressure of a portion of elder-pith, presenting a surface of nearly one-third of an inch square, and weighing only 1-33rd of a grain (2 mgrm.), could be distinguished; whilst the tips of the fingers required a weight, presenting the same superficies, of 1-3rd of a grain or more, and the toes as much as 8 grains, before any sensation of pressure was felt. The presence of the minute hairs on the face was, however, found materially to augment its sensibility, since when these were shaved off it was much diminished.—According to Weber, differences in the amount of pressure are more accurately distinguished if they are applied successively to the same point, than if they are estimated coetaneously. The interval, however, must not be more than a few seconds, unless the difference be considerable. Thus, when 4 ounces and 5 ounces were successively applied, an accurate judgment of the difference might be made after 90 seconds; but the difference between 14·5 and 15 ounces could not be accurately determined after 40 seconds. If the bare sense of pressure were assisted by the muscular sense, as in cases when the hand was unsupported, much finer discrimination was always displayed. Thus on lifting a cloth in which weights were concealed, Weber found that ten people correctly indicated that a weight of 80 ounces was heavier than one of 78 ounces. Both Weber and Fechner† appear to have satisfactorily shown that with light weights smaller differences are perceived than with heavy weights. Thus supposing that *ounce* weights are distinguishable in the ratio of 29 to 30—*i.e.*, that a weight of 29 ounces can be discriminated when attentively examined from one of 30 ounces, a whole ounce requiring to be added or substracted before certainty is attained; when *drachms* are employed the same ratio still subsists, so that in this instance the removal or addition of one drachm to a weight of 30 drachms can be accurately appreciated. Dohrn endeavoured to ascertain the smallest additional weight that could be perceived by different parts of the body loaded with a weight of one gramme. He found that for the third phalanx of the fingers it was 0·499 gramme, for the dorsum of the foot 0·5 gramme, for the second phalanx of the fingers it was 0·771 gramme, for the first phalanx of the fingers it was 0·82 gramme, for the lower part of

* Auber and Kammler, Moleschott's "Untersuch.," Band v. p. 145; Dohrn, "Zeits. f. rat. Med.," 1860. † "Elemente der Psychophysik," 1860.

the thigh 1 gramme, for the back part of the hand 1·156 grammes, for the fore-arm 1·99 grammes, for the sternum 3 grammes, for the umbilical region 3·5 grammes, and for the back 3·8 grammes. Meissner has drawn attention to the fact, which must be familiar to most persons, that if the hand or foot be immersed in warm water or mercury, the only sensation experienced is that of a ring surrounding the limb at the surface of the fluid. The effect is, as he suggests, probably due to the circumstance that the pressure is applied in such cases with perfect uniformity over the part immersed, and therefore causes no disturbance of the nervous elements, the tactile sense being only excited at the line where the pressure produced by the fluid is that exchanged for that of the air.—Valentin* has endeavoured to ascertain the duration of a momentary excitation of the sense of Touch by rolling a spiked wheel over the skin; when slowly rotated, the contact of each spike was clearly discerned; but when only 1-640th of a second intervened between the successive blows, they could no longer be distinguished.—M. Lalanne,† adopting the same method, found the duration of tactile sensations to be considerably greater. The shortest duration observed was about 1-24th or 1-25th of a second, and it never surpassed 1-10th; some differences occurred, according to the individaul and the part of the body experimented on.—That the conditions under which certain of the modifications of common sensation operate, are in some respects different from those of ordinary Touch, is very easily shown. Thus, the feeling of tickling is excited most readily in parts which have but a low tactile sensibility—namely, the armpits, flanks, and soles of the feet; whilst in the points of the fingers, whose tactile sensibility is most acute, it cannot be excited. Moreover, the nipple is very moderately endowed with ordinary sensibility; yet by a particular kind of irritation, a very strong feeling may be excited through it.—Again, in regard to Temperature, it is remarked by Weber that the left hand is more sensitive than the right; although the sense of touch is undoubtedly the most acute in the latter. He states that if the two hands, previously of the same temperature, be plunged into separate basins of warm water, that in which the left hand is immersed will be felt as the warmer, even though its temperature is somewhat lower than that of the other. In regard to the sensations of heat and cold, he points out another curious fact—that a weaker impression made on a large surface seems more powerful than a stronger impression made on a small surface; thus, if the forefinger of one hand be immersed in water at 104°, and the whole of the hand be plunged in water at 102°, the cooler water will be thought the warmer; whence the well-known fact, that water in which a finger can be held will scald the whole hand. Hence it also follows, that minute differences in temperature, which are imperceptible to a single finger, are appreciated by plunging the whole hand in water; in this manner a difference of one-third of a degree may readily be detected, when the same hand is placed successively in two vessels. The judgment is more accurate, when the temperature is not much above or much below the usual heat of the body; just as sounds are best discriminated, when neither very acute nor very grave.

551. The pathological observations of M. Brown-Sequard‡ strongly support the view that separate conductors for sensations of pain, tickling, and temperature do exist, and he even believes he has demonstrated that the nerves conducting these four kinds of impression from the inferior extremities and

* 'Ueber die Dauer der Tasteindrücke,' "Archiv f. Physiol. Heilk," Band xi. p. 438.

† Robin's "Journal de l'Anatomie," 1876, p. 452.

‡ "Archives de Physiologie," 1868, vol. i. p. 610; see also Sieveking, "Med.-Chir. Rev.," 1858, p. 280: Spring, "Presse Médicale," 1864, No. xxxiv.

greater part of the trunk after decussation are situated in the upper part of the Spinal cord, behind the corresponding group belonging to the upper limbs and the neck. Horvath* has made the curious observation, that if the fingers be kept for some time in alcohol, only a few degrees (8°) above the freezing point, whilst the tactile sensibility is retained, the prick of a needle is not felt. The experiments made by Weber† to determine whether there are special conductors for temperature, in which he applied spatulas of different temperature (48° and 122° F.) to the surface of the skin denuded of its integument by a burn, and found that only pain was experienced, are of little value. It is remarkable, however, that we cannot excite impressions of heat or cold by direct application to the trunks of nerves which we know must conduct such impressions; for the parts of the skin, immediately beneath which lie large nerve-trunks, are not more sensitive to moderate heat and cold than are any others; whilst a greater degree of either is felt as pain, not as a change of temperature. Thus, a mixture of ice and water applied over the ulnar nerve affects it in fifteen seconds, and produces severe pain, having no resemblance to cold, and such as cannot be excited by the same degree of cold applied to any other region. So the nerve of the tooth-pulp is equally and similarly affected by water of 43° and of 112°; either application causing a pain exactly similar to that excited by the other, or to that produced by pressure. The same is true of the impressions received through the skin itself, when they pass beyond certain limits of intensity; thus, the sensation produced by touching frozen mercury is said to be not distinguishable from that which results from touching a red-hot iron. Wunderli‡ and Fick, moreover, found that sensations of heat, even in the most sensitive parts of the body, were sometimes mistaken for those of contact. Thus, in the case of the hand, an erroneous conclusion was arrived at six times out of 105 trials, and on the back twelve times in 30 experiments. The perception of variations of temperature does not extend in the mucous membranes far beyond their external orifices; and Weber found that on drinking a tumbler of water at 32° F., he felt the cold water in the mouth and pharynx, though its passage into the stomach could not be perceived. There was, it is true, a slight sensation of cold in the gastric region, but as it only occupied the situation of the anterior wall of the stomach, it was attributable to the abstraction of heat from the abdominal integuments in contact with this. On drinking three glasses of milk at 158°, 145°, and 140°, the sensation of heat could not be traced lower down than that of the cold in the previous experiment. In like manner, the injection of fourteen ounces of water at 65° into the rectum, produced scarcely any sensation of cold, though on its return, a few minutes afterwards, a distinct feeling of cold at the anus. When water at so low a temperature as 45·5° F. was injected, the first feeling excited was a sensation of cold in the immediate neighbourhood of the anus, and then a feeble movement in the bowels; but, a little time afterwards, there was a faint sensation of cold, especially in the anterior wall of the abdomen. This sensation, however, remained after the return of the water; and may hence be attributed to the abstraction of warmth from the abdominal integuments, which was proved to have taken place, the temperature of the surface being lowered 3°. So, again, if the cavity of the nose be filled with cold water, the coldness is only perceived in the parts of the cavity which are most endowed with the proper tactile sense—namely, the neighbourhood of the nostrils and

* "Centralblatt," 1873, p. 208. † Müller's "Archiv," 1849, p. 273.
‡ Henle and Meissner's "Bericht," 1859, p. 632.

of the pharynx; and it is not at all discernible in the higher part of the cavity, which is especially subservient to the olfactory sense. But when the water injected is very cold (*e.g.* 41°), a peculiar pain is felt in the upper part of the nasal fossæ, extending to the regions of the forehead and the lachrymal canals; this pain, however, is altogether different from the sense of coldness. The eyelids, cheeks, and temples, can distinguish variations of temperature amounting to not more than from 0·4° to 0·2° C. The hand and finger are about equally sensitive, but are less so than the forearm, and this again is exceeded by the upper arm, which can distinguish a difference of 0·2° C., and the same holds good of the foot, leg, and thigh. In Nothnagel's* extensive series of experiments, it was found that slight differences of temperature are most acutely recognized between 80° and 91° Fahr.

552. The improvement in the sense of Touch, in those persons whose dependence upon it is increased by the loss of other senses, is well-known; and the remarkable circumstance noticed by Volkmann,† that the increased sensitiveness which results from frequent experiments made upon one side of the body is experienced also in the nerve-fibres distributed to the opposite and exactly symmetrical parts, seems to show that the improved delicacy of the sense is to be in part attributed (as already remarked) to the increased attention which is given to the sensations, and in part, it may be surmised, to an increased development of the tactile organs themselves, resulting from the frequent use of them. The process of the acquirement of the power of recognizing elevated characters by the touch, is a remarkable example of this improvability. When a blind person first commences learning to read in this manner, it is necessary to use a large type; and every individual letter must be felt for some time, before a distinct idea of its form is acquired. After a short period of diligent application, the individual becomes able to recognize the combination of letters in words, without forming a separate conception of each letter; and can read line after line, by passing the finger over each, with considerable rapidity. When this power is once thoroughly acquired, the size of the type may be gradually diminished: and thus blind persons may bring themselves, by sufficient practice, to read a type not much larger than that of an ordinary large-print Bible. The case of Saunderson, who, although he lost his sight at two years old, became Professor of Mathematics at Cambridge, is well-known; amongst his most remarkable faculties, was that of distinguishing genuine medals from imitations, which he could do more accurately than many connoisseurs in full possession of their senses. Several instances are recorded of men who became eminent as sculptors after the loss of their sight, and who were particularly successful in modelling portrait-busts; hence, it is obvious, not merely the *tactile* but the *muscular* sensibility must be greatly augmented in acuteness by the habit of attending to it. The power of immediate recognition of individuals by the slightest contact of the hands, even after long periods of time, which most blind and deaf persons have displayed, is one of the most curious examples of the mode in which tactual perceptions will impress themselves on the memory, when they are habitually attended to. As an example of the correct notions which may be conveyed to the mind, of the forms and surfaces of a great variety of objects, and of the sufficiency of these notions for accurate comparison, the Author may mention the case of a blind friend of his own who has acquired a very complete knowledge of conchology, both recent and fossil; and who is not only able to

* "Deutsches Archiv f. Klin. Med.," Band ii. p. 284.

† Volkmann, "Uber der Einfluss der Uebung auf das Erkennen raümlicher Distanzen," "Bericht der Sachs. Gesell.," 1858.

recognize every one of the numerous specimens in his own cabinet, but to mention the nearest alliances of a shell previously unknown to him, when he has thoroughly examined it by his touch. Many similar instances might be cited, one of the most remarkable being that of John Gough, who, although blind, was a noted botanical collector, and earned his livelihood as a land surveyor. Several cases are on record* of the acquirement by the blind of the power of distinguishing the *colours* of surfaces which were similar in other respects, and, however wonderful this may seem, it is by no means incredible. For it is to be remembered, that the difference of colour depends upon the position and arrangement of the particles composing the surface, which render it capable of reflecting one ray whilst it absorbs all the rest; and it is quite consistent with what we know from other sources, to believe that the sense of Touch may become so refined, as to communicate a perception of such differences.†

3. *Sense of Taste.*

553. The sense of Taste is that by which we distinguish the *sapid* properties of bodies. The term, as commonly understood, includes much more than this; being usually employed to designate the whole of that knowledge of the qualities of a body (except such as is purely tactile), which we derive through the sensory apparatus situated within the mouth. But it will be hereafter shown that a considerable part of this is dependent upon the assistance of the *olfactive* sense (§ 559); which is affected, through the posterior nares, by the odorous emanations of all such bodies as are capable of giving them off; and the indications of which are so combined with those of the true gustative sense, as to make an apparently single impression upon the Sensorium. Moreover, there are certain sensorial impressions received through the organ of taste, which are so nearly allied in their character to those of *touch*, as to render it difficult to specify any fundamental difference between them; such are the *pungent* sensations produced by mustard, pepper, the essential oils, &c.; all of which substances, when applied for a sufficient length of time to any part of the cutaneous surface, produce a sensation which can scarcely be distinguished from that excited through the organ of taste, in any other way than by its inferior intensity, and by the absence of the concurrent odorous emanations. The *taste* of such substances might therefore, perhaps, be considered as the composite result of the impressions made upon the sensorium through a refined and acute *touch*, and by the effect of their odorous emanations upon the organ of *smell*. After making full allowance, however, for all such as can be thus accounted for, there remains a large class of pure *sapors*, of which we take cognizance without the assistance of smell, and which are altogether dissimilar to any tactile impressions; such are the *bitter* of quinine, the *sour* of tartaric acid, the *sweet* of sugar, the *saline* of common salt, &c. The smell can give us no assistance in distinguishing small particles of these bodies, since they are either entirely inodorous, or so nearly so, as only to be recognizable through its means when in large masses; and the most refined touch cannot afford any indication of that kind of difference among them, of which we are at once rendered cognizant by taste.—Of all the 'special' senses, however, that of Taste is most nearly allied to that of touch,

* Among the best authenticated of these, is that of a lady who became blind, and afterwards deaf, in consequence of an attack of confluent small-pox; cited in Dr. Kitto's "Lost Senses," vol. ii. p. 79, from the "Annual Register" for 1758.—Dr. Kitto's treatise may be referred to, as containing a large collection of interesting cases of a similar description.

† For some additional details in regard to the sense of Touch, see the Author's article "Touch" in the "Cyclopædia of Anatomy and Physiology," vol. iv.

as appears from several considerations. In the first place, the *actual contact* of the object of sense with the organ through which the impresssion is received, is necessary in the present case, as in the preceding. Again, it appears from the considerations formerly adduced (§ 493), that there is no special nerve of Taste; for the gustative impressions upon the front of the tongue are conveyed by the Lingual branch of the Fifth pair, and the branches of the Facial running in the Chorda tympani,* whilst those made upon the back of the organ are conveyed by the Glosso-pharyngeal, both of which nerves also minister to common sensibility; and pressure on the trunk of either of these nerves gives rise to pain, which is not the case with either the olfactory, the optic, or the auditory nerves. Moreover, the papillary apparatus, through which the gustative impressions are made upon the extremities of these nerves, is essentially the same in structure with that of the skin.†

554. For the Gustative nerve-fibres to be impressed by the distinctive properties of sapid substances, it appears requisite that these substances should be brought into immediate relation with them, and that they should penetrate, in the state of solution, through the investments of the papillæ, into their substance. This would seem to be proved by the two following facts: first, that every substance, whether solid, fluid, or gaseous, which possesses a distinct taste, is more or less soluble in the fluids of the mouth, whilst substances which are perfectly insoluble do not make their presence known in any other way than through the sense of touch; and, second, that if the most sapid substance be applied in a dry state to the papillary surface, and this be also dry, no sensation of taste is excited. Hence it may be inferred that in the reception of gustative impressions, a change is produced in the molecular condition of the nerve-fibres, or, to use the language of Messrs. Todd and Bowman, their polarity is excited by the direct agency of the sapid matter itself. This change may be induced, however, both by electrical and by mechanical stimulation. If we make the tongue form part of a galvanic circuit, a peculiar sensation is excited, which is certainly allied rather to the gustative than to the tactile, and which does not seem to be due (as was at one time supposed) to the decomposition of the salts of the saliva. And, as Dr. Baly has pointed out,‡ "if the end of the finger be made to strike quickly, but lightly, the surface of the tongue at its tip, or its edge near the tip, so as to affect not the substance of the organ, but merely the papillæ, a taste sometimes acid, sometimes saline, like the taste produced by electricity, will be distinctly perceived. The sensation of taste thus induced will sometimes continue several seconds after the application of the mechanical stimulus." On the other hand, as

* Lussana, "Centralblatt f. d. Med. Wiss.," 1871, p. 233.

† For some pathological cases bearing upon the question of the implication of the chorda tympani in the sense of taste, see Inzani and Lussana, in the "Annali Universali di Med.," 1862, pp. 282–322; Stich, in Henle and Meissner's "Bericht," 1857, p. 588; whilst for experimental evidence to the same effect, see Schiff, "Untersuch. zur Naturlehre," Band x. p. 406, and E. Neumann, "Königsberger Medic. Jahrb.," Band iv. p. 1. The two former observers believe the chorda tympani to be the true nerve of taste for the anterior part of the tongue, by which sweet, saline, piquant, and aromatic flavours are distinguished, whilst the mineral acids, astringents, bitters, pungent, putrefactive, and disgusting flavours are chiefly perceived through the glosso-pharyngeal. Schiff, "Physiologie," 1859, p. 403, thinks the Glosso-pharyngeal nerves are especially adapted to perceive bitter, and the Fifth nerves, acid tastes. Moos, "Centralblatt," 1867, No. 46, records a case where modifications of the sense of taste in the fore part of the tongue resulted from pressure on the chorda tympani, occasioned by the use of one of Toynbee's artificial tympana. Blau could excite a sourish taste and a quivering sensation by mechanical stimulation of the chorda tympani in a patient with perforation of the membrana tympani. "Berlin. Klin. Wochensch.," 1875, No. 45.

‡ Translation of Müller's "Physiologie," p. 1062, *note*.

Wagner has truly remarked, if the surface of the tongue near the root be touched with a clean dry glass rod, or a drop of distilled water be placed upon it, a slightly bitterish sensation is produced; and this, if the pressure be continued, passes into that of nausea, and if the pressure be increased, even excites vomiting. The feeling of nausea may be excited by mechanical irritation of any part of the surface of the fauces or soft palate; and this feeling is certainly much more allied to that of taste than to that of touch. Further, it has been observed by Henle, that if a small current of air be directed upon the tongue, it gives rise to a cool saline taste like that of saltpetre. Thus we find that the peculiar effects of sapid substances upon the nerves of taste may be imitated to a certain extent by other agencies; and it also appears that the sensations excited by these vary according to the part of the gustative surface on which they operate; mechanical or electrical stimulation of the front of the tongue giving rise to a kind of saline taste, whilst mechanical stimulation applied to the back of the tongue and fauces excites the feelings of bitterness and nausea.—One of the conditions requisite for the due exercise of the gustative sense is, a temperature not departing far on either side from that which is natural to the body. It appears from the experiments of Professor E. H. Weber,* that if the tongue be kept immersed for nearly a minute in water of about 125°, the taste of sugar brought in contact with it, either in powder or solution, is no longer perceived; the sense of touch, usually so delicate at the tip of the tongue, being also rendered imperfect. A similar imperfection of taste and touch was produced by immersing the tongue for the same length of time in a mixture of water and broken ice.

555. The surface of the Tongue is undoubtedly the special seat of gustative sensibility in Man; though the sense of Taste is not by any means restricted to that organ, being diffused in a less degree over the soft palate, the arches of the palate, and the fauces. It is on the tongue alone, however, that the papillary apparatus is fully developed; and its structure has been so carefully examined and described by Messrs. Todd and Bowman,† that little remains to be added to their account of it.—The lingual papillæ may be divided, in the first place, into the *Simple* and the *Compound*, the former of which had previously escaped observation, through not forming any apparent projection. The *Simple* papillæ are scattered, in the intervals of the compound, over the general surface of the tongue; and they occupy much of the surface behind the circumvallate variety, where no compound papillæ exist. They are completely buried and concealed beneath the continuous sheet of epithelium, and can only be detected when this membrane has been removed by maceration; they are then found to have the general characters of the cutaneous papillæ. The *Compound* papillæ are visible to the naked eye; and have been classified, according to their shape, into the *circumvallate*, the *fungiform*, and the *filiform*. The *circumvallate* or calyciform papillæ are eight or ten in number, and are situated in a V-shaped line at the base of the tongue. Each consists of a central flattened circular projection of the mucous membrane, surrounded by a tumid ring of about the same elevation, from which it is separated by a narrow circular fissure. The surface of both centre and border is smooth, and is invested by scaly epithelium, which conceals a multitude of simple papillæ. The *fungiform* papillæ, varying in number from 160 to 290,‡ are scattered singly over the tongue, chiefly upon its sides and tip. They project

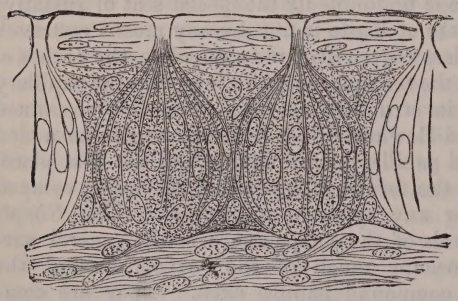
* Müller's "Archiv," 1847, s. 342.
† "Physiological Anatomy and Physiology of Man," vol. i. chap. xv.
‡ Szabadföldy, Virchow's "Archiv," xxxviii. p. 177.

considerably from the surface, and are usually narrower at their base than at their summit. They contain a complex capillary plexus (Fig. 252), the terminal loops of which enter the numerous simple papillæ that clothe the surface of the fungiform body. Amidst these lie nerve-tubes, which probably terminate in free extremities between the epithelial cells, the epithelium itself being so thin as to allow the red colour of the blood to be seen through it. In this manner they are readily distinguished from the filiform papillæ among which they lie. The *filiform* papillæ, like the preceding, contain a plexus of capillaries and a bundle of nerve-fibres, both terminating in loops, which enter the simple papillæ that clothe the surface of the compound body; but instead of being covered with a thin scaly epithelium, they are furnished with bundles of long pointed processes, some of which approach hairs in their stiffness and structure. These are immersed in the mucus of the mouth, and may be moved in any direction, though they are generally inclined backwards.—The simple papillæ which occur in an isolated manner, may not improbably be tactile; while those which are aggregated in the circumvallate and fungiform bodies, doubtless minister to the sense of Taste, this being most acute in the situations wherein they most abound. With regard, however, to the office of the filiform papillæ, there seems much reason to coincide in the opinion of Messrs. Todd and Bowman:—"The comparative thickness of their protective covering, the stiffness and brush-like arrangement of their filamentary productions, their greater development in that portion of the dorsum of the tongue which is chiefly employed in the movements of mastication, all evince the subservience of these papillæ to the latter function, rather than to that of taste; and it is evident that their isolation and partial mobility on one another must render the delicate touch with which they are endowed more available in directing the muscular actions of the organ. The almost manual dexterity of the organ, in dealing with minute particles of food, is provided for, as far as sensibility conduces to it, in the structure and arrangement of these papillæ. It may be added, that the filiform papillæ of Man seem to be the rudimentary forms of those horny epithelial processes which acquire so great a development in the tongues of the Carnivora, and which are of such importance in the abrasion of their food. The mode of termination of the gustatory nerves has been the subject of much recent research. Engelmann* describes the glosso-pharyngeal nerves in Man and Mammals as terminating in peculiar organs, termed

Fig. 252.

Capillary plexus of *fungiform papilla* of the Tongue.

Fig. 253.

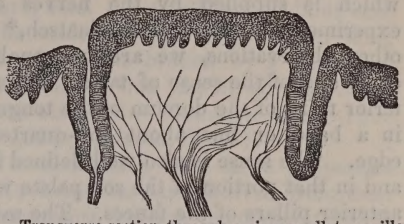


Gustatory bulbs from the lateral gustatory organ of the Rabbit. Mag. 450 diam.

* Stricker's "Manual of Histology," New Sydenham Society, 1853, vol. iii. p. 1, where a complete bibliography of the subject is given. The principal English references are Waller, "Philosophical Transact.," 1847; Lionel Beale, idem. 1865, and "Quart. Journ. of Microscop. Soc.," 1869; and R. L. Maddox, "Month. Microscop. Journal," 1869. And since the date of Engelmann's article, the following papers have appeared:—Ajtai, "Archiv f. Mic. Anat.," Band viii. p. 455; Ditlevsen, "Undersögelse," &c., Copenhagen, 1872;

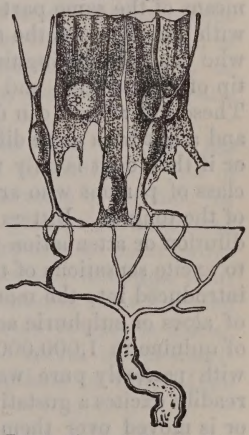
gustatory bulbs, or taste-buds. These are flask-shaped bodies (Fig. 253), which are disposed in a zone encircling the sides of the papillæ circumvallatæ (Fig. 254), a few being also found on the outer wall of the vallecula, or that which looks towards the papilla. Schwalbe estimated the number present in one circumvallate papilla of the Sheep at 480, and in one such papilla from the Ox at 1760. They are also found, but more irregularly distributed, upon the fungiform papillæ. The bulbs are composed of groups of cells (Fig. 253), which occupy flask-shaped cavities in the mucous membrane. The bottom of the cavity is formed by the fibrous layer of the mucous membrane, its sides are composed of cells, and the slender short neck perforates the corneal lamina, opening on the surface by a small circular mouth, which may be called the *gustatory pore.* The length of the bulb is about 0·080 of a millimeter. The gustatory bulbs, which completely fill these spaces, are composed of two kinds of cells. Of these the outer, or *investing cells* (Fig. 255), from 15 to 30 in number, are fusiform, have a well-defined nucleus, and are arranged concentrically to the surface in closely-compressed rows. They enclose a group of cells which are believed to be the *true gustatory cells.* These have a long and thin body, with a large vesicular nucleus, from which a peripheric process runs, that either ends by an abruptly truncated extremity (rod or staff-cell), or in a very fine point (needle-cells), the apices projecting for some distance through the gustatory pore. The relations of these organs to the gustatory nerves has not been quite satisfactorily made out; but the finely medullated branches of the glosso-pharyngeal nerve, containing small groups of ganglion-cells, have been observed to form plexuses beneath the papillæ, from which one or more fasciculi are given off, that run up the axis of the papilla, and then break up into numerous fine branches which stream out towards the epithelium. In the Frog, cylindrical papillæ are present, which are composed below of loose, and near their free extremity of compact, connective tissue, forming a *nerve-cushion;* upon each of these lies a gustatory disc, the structure of which is analogous to that of the gustatory bulb, being resolvable into *goblet* and *columnar* supporting or protecting cells, and *forked* cells, which appear to be the continuation of the non-medullated nerve-fibres (Fig. 255).

Fig. 254.



Transverse section through a circumvallate papilla of a Calf, showing the arrangement of the gustatory bulbs.

Fig. 255.



Termination of the gustatory nerves of the Frog. Ramification of a nerve-fibre in the nerve-cushion. Two goblet cells are seen, one columnar, and ten forked cells. (Chromic acid and glycerine. Mag. 600 diam.)

556. The simple application of a sapid substance to the gustative surface is usually sufficient to excite the sensation; and if this application be restricted to one particular spot, we are able to recognize its place more or less distinctly. In this respect, then, the gustative impression resembles

Abstract in Schwalbe's "Jahresbericht," 1872. Hönigschmeid, "Zeitsch. für wiss. Zool.," Band xxiii. p. 414 and Band xxix. p. 255; Sertoli, "Gazetta Med.-Vet.," Anno iv. Sep. Abd. Leydig, see Ref. in Hofmann's "Jahres bericht," 1879, i. p. 31.

the tactile; for whilst we cannot by our own consciousness distinguish the parts of the retina or of the auditory apparatus on which visual or auditory impressions are made, we can make this distinction in regard to the surface which is supplied by the nerves of general sense. From the careful experiments of Stich and Klaatsch,* supported as they are by the results of other observations, we are now enabled to define with some accuracy the exact seat of the sense of taste. It exists over the whole surface of the posterior third of the dorsum of the tongue, on the under surface of the tip, and in a band or line, about one-quarter of an inch broad, running along its edge. The sense is also well defined in the posterior part of the hard palate, and in that portion of the soft palate which is near the bone, and lastly, in the anterior pillars of the fauces. The middle and anterior part of the dorsum, the gums, posterior pillars of the fauces, and the inner surface of the lips, possess no sense of taste, though exquisitely sensitive to tactile impressions. M. v. Vintschgau,† in summing up the results obtained by himself and other physiologists, has come to the following conclusions in regard to the sensation of Taste by the tip of the tongue. He finds that there are some persons who can distinguish all the chief sensations of Taste solely by the tip of the tongue. There are other persons who can perceive with certainty by means of the same part the sensations of sweetness, saltness, and acidity, but with less clearness the sensation of bitterness. There are again other persons who can only distinguish individual tastes with the greatest difficulty by the tip of the tongue, and to this category M. v. Vintschgau himself belongs. These individuals can distinguish an acid from a sweet with comparative ease, and a salt with more difficulty, but they either entirely fail to perceive a bitter, or if they do it is only with the utmost attention. Lastly, there is still another class of persons who are wholly incapable of perceiving any taste by the tip of the tongue. Bitters and acids appear to be the substances of which the dilution or attenuation may be carried to the greater extent, without ceasing to excite sensations of taste, providing a sufficient volume of the solution be introduced into the mouth. Thus, according to Valentin, one part of extract of aloes or sulphuric acid in 900,000 of water, and even one part of sulphate of quinine in 1,000,000 of water, may be distinguished if heedfully compared with perfectly pure water. The contact of a sapid substance much more readily excites a gustative sensation, when it is made to press upon the papillæ, or is moved over them. Thus there are some substances whose taste is not perceived when they are simply applied to the central part of the dorsum of the tongue, but of whose presence we are at once rendered cognizant by pressing the tongue against the roof of the mouth. The full flavour of a sapid substance, again, is more readily perceived when it is rubbed on any part of the tongue, than when it is simply brought in contact with it, or pressed against it, and Camerer has shown that the intensity of the gustatory sensations depends partly on the number of papillæ that are stimulated, and partly‡ upon the degree of concentration of the solution. Hence, when liquids are received into the mouth their taste is most completely discriminated by causing them to move over the gustative surface: thus the 'wine-taster' takes a small quantity of the liquor into his mouth, carries it rapidly over every part of its lining membrane, and then ejects it. It is not improbable that this exaltation of the usual effects is simply due to mechanical causes; the sapid particles being brought by the pressure or movement into more rapid and complete operation on the nerve fibres, than they would be if simply

* "Archiv f. Path. Anat.," Band xiv. 1858, p. 225, and Band xviii. p. 80.
† Pflüger's "Archiv," Band xiv p. 443. ‡ Camerer, "Zeits. f. Biologie," Band vi p. 440.

placed in contact with the papillæ. The rapidity with which sapid impressions are perceived has been made the subject of a series of experiments by Vintschgau and Hönigschmied.* The substances used were bisulphate of quinine, sugar, common salt, and diluted phosphoric acid. A small brush, about one-third of an inch square, was applied to the surface of the tongue. On being applied, an electrical current was made, which was broken by a movement of the hand as soon as the taste was perceived. When the tip of the tongue was thus excited, the following times were obtained:—Common salt, 0·1598 sec.; sugar, 0·1639; phosphoric acid, 0·1676; quinine, 0·2351.

557. The impressions made upon our consciousness by a large proportion of sapid substances are of a complex kind; being in part derived from their odorous emanations, of which we take cognizance through the organ of Smell. Of this any one may convince himself by closing the nostrils, and inspiring and expiring through the mouth only, whilst holding in the mouth, or even rubbing between the tongue and the palate, some aromatic substance; for its taste is then scarcely recognized, although it is immediately perceived when its effluvia are drawn into the nose. It is well known too, that when the sensibility of the Schneiderian membrane is blunted by inflammation (as in an ordinary 'cold in the head'), the power of distinguishing flavours is very much diminished. In fact, some physiologists are of opinion that *all* our knowledge of the *flavour* of sapid substances is received through the Smell; but this, as already shown, would not be a correct statement; and there are cases on record in which the sense of smell has been entirely lost, without any impairment of the true sense of Taste.†

558. Taken in its ordinary composite acceptation, the sense of Taste has for its object to direct us in the choice of food, and to excite the flow of mucus and saliva, which are destined to aid in the preparation of the food for Digestion. Among the lower animals, the instinctive perceptions connected with this sense are much more remarkable than our own; thus an omnivorous Monkey will seldom touch fruits of a poisonous character, although their taste may be agreeable; and animals whose diet is restricted to some one kind of food will decidedly reject all others. As a general rule it may be stated, that substances of which the taste is agreeable to us are useful in our nutrition, and *vice versâ*:‡ but there are many signal exceptions to this.—Like

* Pflüger's "Archiv," 1875, pp. 1–48.

† An interesting case of this kind, occurring in a Negro who had gradually lost the characteristic hue of his skin, and had acquired the fair complexion of a European, has been put on record by Dr. J. C. Hutchinson.—The Olfactory nerve seemed to be entirely paralyzed, whilst the branches of the Fifth Pair retained their integrity; so that, whilst the proper sense of Smell was entirely lost, a pungent burning sensation was excited by irritating vapours, and the application of snuff induced sneezing. Notwithstanding this deficiency, the sense of Taste, properly so called, did not seem to be impaired; for substances which possessed neither odour nor pungency could readily be discriminated, even though their tastes were not widely different. (See "Amer. Journ. of Med. Sci.," Jan. 1852.)

‡ It is justly remarked by Sir H. Holland ("Medical Notes and Reflections," p. 85) that,—"In the majority of instances of actual illness, provided the real feelings of the patient can be certainly ascertained, his desires as to food and drink may be safely complied with. But undoubtedly much care is needful that we be not deceived as to the state of the appetites, by what is merely habit or wrong impression on the part of the patient, or the effect of the solicitation of others. This class of sensations is more nurtured out of the course of Nature than are those which relate to the temperature of the body. The mind becomes much more deeply engaged with them; and though in acute illness they are generally submitted again to the natural law, there are many lesser cases where enough remains of the leaven of habit to render every precaution needful. With such precautions, however, which every physician who can take schooling from experience will employ, the stomach of the patient becomes a valuable guide; whether it dictate abstinence from a recurrence of food; whether much or little in quantity; whether what is solid or liquid; whether much drink or little; whether

other senses, that of Taste is capable of being rendered more acute by education; and this on the principles already laid down in regard to Touch. The experienced wine-taster can distinguish differences in age, purity, place of growth, &c., between liquors that to ordinary judgments are alike; and the epicure can give an exact determination of the spices that are combined in a particular sauce, or of the manner in which the animal on whose flesh he is feeding was killed. As in the case of other senses, moreover, impressions made upon the sensory surface remain there for a certain period; and this period is for the most part longer than that which is required for the departure of the impressions made upon the eye, the ear, or the organ of smell. Every one knows how long the taste of some powerful substances remains in the mouth; and even of those which make less decided impressions, the sensations remain to such a degree that it is not difficult to compare them at short intervals. Hence if a person be blindfolded, and be made to taste substances of distinct, but not widely-different flavours (such as various kinds of wine or spirituous liquors), one after another in rapid succession, he soon loses the power of discriminating between them. In the same manner, the difficulty of administering very disagreeable medicines may be sometimes got over, by either previously giving a powerful aromatic, or by combining the aromatic with the medicine; its strong impression in both cases preventing the unpleasant taste from exciting nausea.

4. *Sense of Smell.*

559. The Nasal passages may be considered as having, in air-breathing Vertebrata two distinct offices; for they constitute the portal of the Respiratory organs, and have for their office to take cognizance of the aëriform matter as it enters them, and to give warning of that which would be injurious (this being effected by the instrumentality of the Fifth pair), which receives the impressions of gaseous irritants, and excites the act of sneezing to expel them; whilst they also contain the organ of Smell, which is formed by the distribution, over a certain part of their membranous wall, of the *Olfactory* nerve, which is susceptible of being impressed by odorous emanations. Of the nature of these emanations the Physical Philosopher is so completely ignorant, that the Physiologist cannot be expected to give a definite account of the mode in which they produce sensory impressions. Although it may be surmised that they consist of particles of extreme minuteness, dissolved as it were in the air, and although this idea seems to derive confirmation from the fact that most odorous substances are volatile, and *vice versâ*—yet the most delicate experiments have failed to discover any diminution in weight, in certain substances (as musk) that have been impregnating a large quantity of air with their effluvia for several years; whilst there are some volatile fluids, such as water, which to man are entirely inodorous. Nearly all the

things warm or cold; whether sweet, acid, or saline; whether bland or stimulating to the taste." Further, Sir H. Holland remarks: "It is not wholly paradoxical to say that we are authorized to give greatest heed to the stomach, when it suggests some seeming extravagance of diet. It may be that this is a mere deprivation of the sense of taste; but frequently it expresses an actual need of the stomach, either in aid of its own functions, or indirectly (under the mysterious law just referred to) for the effecting of changes in the whole mass of blood. It is a good practical rule in such cases to withhold assent, till we find after a certain lapse of time that the same desire continues or strongly recurs; in which case it may generally be taken as the index of the fitness of the thing desired for the actual state of the organs. In the early stage of recovery from long gastric fevers, I recollect many curious instances of such contrariety to all rule being acquiesced in, with manifest good to the patient. Dietetics must become a much more exact branch of knowledge before we can be justified in opposing its maxims to the natural and repeated suggestions of the stomach, in the state either of health or disease.

vegetable odours belong to one or other of three categories—namely, hydrocarbons, aldehydes, or ethers. Many of them are capable of being artificially formed, and they present good examples of Isomerism. Thus the essences of turpentine, citron, bergamot, neroli, juniper, savin, lavender, cubebs, peppermint, and cloves, all have the same composition, C_{10} H_{16}. Amongst the odoriferous essences that are ranged by chemists in the class of aldehydes are those of mint, rue, bitter almonds, cummin, anise, fennel, canella, and meadow-sweet. The ethers are very varied and complex in constitution. Linnæus arranged odours into seven classes:—Aromatic (laurel leaves); fragrant (jasmine); ambrosial (musk); alliaceous (garlic); fetid (stinking goosefoot); repulsive (solanaceæ); and nauseous odours. Such an arrangement is very imperfect, not including, for example, such well-marked odours as those of tar gas.* Prévost† has described two phenomena that are presented by odorous substances, the observation of which he has termed *odoroscopy*. One is, that odorous substances when placed on water begin, like particles of camphor, to move, owing to their emission of an elastic fluid into the air, and the other is that a thin layer of water, extended on a perfectly clean glass plate, retracts when such an odorous substance as camphor is placed upon it. Liegeois has further shown that the particles of an odorous body placed on water undergo a rapid division, and that the movements of camphor, or of benzoic acid, are inhibited, or altogether arrested if an odorous substance be brought into contact with the water on which they are moving.‡ The original motion of camphor he attributes to its emitting an oily fluid.§

560. The tractus olfactorius is exclusively composed of medullated nerve fibres which have a sheath of Schwann. It terminates on each side in the Olfactory ganglion, from which the Olfactory nerves pass down in the form of very numerous minute threads, which form a plexus upon the surface of the Schneiderian or pituitary membrane (Fig. 256.) The filaments composing this plexus are described by Messrs. Todd and Bowman‖ as differing widely in structure from those of the ordinary cephalic nerves; they contain no white substance of Schwann, are nucleated and finely granular in texture, and altogether bear a close resemblance to the gelatinous form of nerve fibres (Fig. 256). The mode in which these nerves terminate has recently been the subject of close investigation by several observers.¶ Their distribution appears to be limited to the membrane covering the upper third of the septum of the nose, the superior turbinated bone, and perhaps the upper part of the middle turbinated bone; together with the upper wall of the nasal cavities beneath the cribriform plate of the ethmoid bone; all which surface is

Fig. 256.

Fibres of ultimate ramifications of *Olfactory Nerve* of Dog.

* See an interesting paper on Odours, by F. Papillon, in "Pharmaceut. Journ.," Nov. 16, 1872, p. 383; also "Lancet," 1870, p. 847.

† Hermann's "Handbuch der Physiologie," Band iii. 1880, pt. ii. p. 263.

‡ Odorous mineral substances do not conform to the above laws, neither does ammonia.

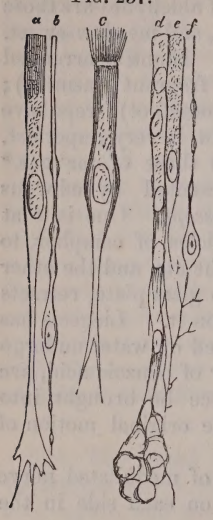
§ In "Heat a Mode of Motion," Tyndall gives a list of the absorptive powers of various odorous substances for heat. See also H. Cloquet, "Osphresiologie."

‖ "Physiological Anatomy," vol. ii. p. 9.

¶ Hoyer, Henle and Meissner's "Bericht," 1857, p. 27; Schultze, "Untersuchungen über den Bau der Nasenschleimhaut," Halle, 4to; Lockhart Clarke, "Zeits. f. wissens. Zool.," Band xi. For an abstract of this paper, see "Med.-Chir. Review" for 1862, vol. i. p. 521. See also Exner, "Sitz. d. k. Akad. zu Wien," 1870 and 1872. Exner denies the distinctness

covered (as Messrs. Todd and Bowman have pointed out) with an epithelium of a rich sepia-brown hue, constituting the *regio olfactoria* of Babuchin. According to Schultze these epithelial cells are divisible into two sets: one of these (*a*, Fig. 257) may be described as terminating externally by truncated flat surfaces which cannot be observed to be covered by any membrane separate from the contents of the cell. The contents themselves appear to consist of protoplasm presenting a yellowish granular appearance in the outer part, whilst at the lower part an oval nucleus lying in clear protoplasm can be readily distinguished. Towards their attached extremity these cells become attenuated, and can be traced inwards for a considerable distance, when they expand into a broad flat sheet or plate, which, whilst it frequently presents a granular appearance, is never coloured. The processes which pass off from this sheet appear to be continuous with the fibres of the submucous connective tissue. Towards the margin of the true olfactory region, cells (*c*, Fig. 257) in every respect analogous to those just described are found, excepting only that they present a well-defined band or seam at their free extremity, which is surmounted by a circle of cilia.—The cells of the second set (*b*, Fig. 257) have been described by Schultze and Babuchin as continuations of the nerves, and have hence been termed by them 'Olfactory cells.' They are thin, fibrous, or rod-like bodies, terminating at the same level as the proper epithelial cells in a leash of long fine cilia (Babuchin), and presenting when traced inwards a large oval nucleus and a series of moniliform or varicose swellings which are directly continuous with outrunners of more deeply seated nerve cells. Closely analogous appearances have been seen and described by Lockhart Clarke, who states that the Olfactory nerve-fibres on reaching the base of the epithelial layer divide into finer and still finer branches, to form a network with numerous interspersed nuclei, through which they are probably connected with the 'Olfactory cells' (*f*, Fig. 257). The proper epithelial cylinders (*d*, *e*) are connected at their bases with the septa formed of connective tissue belonging to the sub-epithelial glandular layer.—The remainder of the nasal surface constituting the 'Regio respiratoria' is supplied by the Fifth pair only, and is not endowed with sensibility to odours, although it is susceptible of irritation from such as are of a pungent nature; and hence it is that we cannot distinguish faint odours, unless, by a peculiar inspiratory effort, we draw the air charged with them to the upper part of the nose. In animals living in the air, it is a necessary condition of the exercise of the sense of Smell, that the odorous matter should be transmitted by a respiratory current through the nostrils, and that the membrane lining these should be in a moist state. Hence by breathing through the mouth, we may avoid being affected by odours even of the strongest and most disagreable kind; and in the first state of a catarrh, when the ordinary mucous secretion is suspended, the sense of Smell is blunted from this cause, as it afterwards is from the excess in the quantity of the fluid, which prevents

FIG. 257.



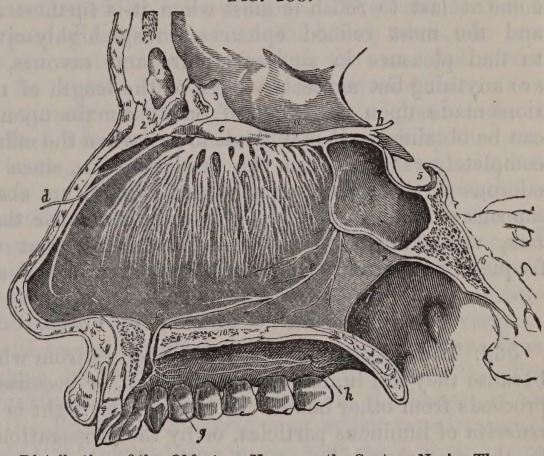
Cells of the Olfactory Mucous Membrane:—*a*, *b*, *c* after Schultze; *d*, *e*, *f* after Lockhart Clarke.

of the two forms of cells described in the text (§ 560); Babuchin, Stricker's "Human and Comp. Histology," Syd. Soc. Trans., 1873, vol. iii. p. 201,; Paschutin, "Leipziger physiol. Arbeiten," 1873, p. 41; Cisoff, "Centralblatt für die Med. Wissenchaften," 1874, p. 689; Martin, "Journ. of Anat. and Physiol.," 1874, vol. viii. p. 39.

the odoriferous effluvia from coming into immediate relation with the sensory extremities of the nerves. Hence we may easily comprehend how sections of the Fifth pair, which exerts a considerable influence over the secretions, will greatly diminish the acuteness of this sense, and will have the further effect of preventing the reception of any impressions of irritation from acrid vapours, which are entirely different in their character from true odorous impressions, and are not transmitted through the Olfactory nerve.

561. The Olfactory nerve can be stimulated by electricity, and by its own special stimuli, but not apparently by heat or by mechanical irritation. Ritter* found that the application of the negative pole to the nose produces a disposition to sneeze, and sometimes a faint smell of ammonia, whilst the positive pole removed the tendency to sneeze, and induced a dull sensation, with sometimes an acid odour. The importance of the sense of Smell among many of the lower Animals, in guiding them to their food, or in giving them warning of danger, and also in exciting the sexual feelings, is well known. To man its utility is comparatively small under ordinary circumstances; but it may be greatly increased when other senses are deficient. Thus, in the well-known case of James Mitchell, who was blind, deaf and dumb, from his birth, it was the principal means of distinguishing persons, and enabled him at once to perceive the entrance of a stranger. It is recorded that a blind gentleman, who had an antipathy for cats, was possessed of a sensibility so acute in this respect, that he perceived the proximity of one that had been accidentally shut-up in a closet adjoining his room. Among savage tribes, whose senses are more cultivated than those of civilized nations, more direct use being made of the powers of observation, the scent is almost as acute as in the lower Mammalia; thus it is asserted by Humboldt, that the Peruvian Indians in the middle of the night can distinguish the different races, whether European, American-Indian, or Negro; and the Arabs of the Great Desert are said to be able to distinguish the smell of a fire thirty miles off.—The quantity of some odorous

Fig. 258.



Distribution of the *Olfactory Nerve* on the Septum Nasi. The nares have been divided by a longitudinal section made immediately to the left of the septum, the right nares being preserved entire.—1. The frontal sinus. 2. The nasal bone. 3. The crista galli process of the ethmoid bone. 4. The sphenoidal sinus of the left side. 5. The sella turcica. 6. The basilar process of the sphenoidal and occipital bones. 7. The posterior opening of the right nares. 8. The opening of the Eustachian tube in the upper part of the pharynx. 9. The soft palate, divided through its middle. 10. Cut surface of the hard palate. *a*. The olfactory peduncle. *b*. Its three roots of origin. *c*. Olfactory ganglion, from which the filaments proceed that spread out in the substance of the pituitary membrane. *d*. The nasal nerve, a branch of the ophthalmic nerve, descending into the left nares from the anterior foramen of the cribriform plate, and dividing into its external and internal branch. *e*. The naso-palatine nerve, a branch of the spheno-palatine ganglion, distributing twigs to the mucous membrane of the septum nasi in its course to (*f*) the anterior palatine foramen, where it forms a small gangliform swelling (Cloquet's ganglion) by its union with its fellow of the opposite side. *g*. Branches of the naso-palatine nerve to the palate. *h*. Posterior palatine nerves. *i, i*. The septum nasi.

* Quoted in Hermann's "Handbuch der Physiologie," 1880, Band iii. pt. ii. p. 255.

bodies which is capable of exciting a distinct perception of Smell, must in some instances be exceedingly small. A very minute trace of sulphuretted hydrogen is readily recognised, and according to Valentin, one part of bromine in 200,000 of air communicates an unpleasant odour to the latter, whilst in the case of musk a proportion not greater than one part in 13,000,000 of air is still perceptible.—The agreeable or disagreeable character assigned to particular odours, is by no means constant amongst different individuals. Just as many of the lower animals pass their whole lives in the midst of odours that are to Man (in his civilized condition at least) in the highest degree revolting, and will even refuse to touch food until it is far advanced in putridity, so do we find that men who are compelled by circumstances to live upon putrescent food, come at last to relish it most when it is furthest advanced in decomposition and the most refined epicures among highly-civilized communities seem to find pleasure in similar odours and savours, which to ordinary tastes are anything but agreeable.—As to the length of time during which impressions made upon the organ of Smell remain upon it, no certain knowledge can be obtained. It is difficult to say when the effluvia themselves have been completely removed from the nasal passages, since it is not unlikely that the odorous particles (supposing such to exist) are absorbed or dissolved by the mucous secretion ; it is probably in this manner that we may account for the fact, well known to every medical man, that the cadaverous odour is frequently experienced for many days after a post-mortem examination.*

5. *Sense of Vision.*

562. The objects of this sense are bodies from which Light proceeds, either because they are luminous in themselves, or because they reflect the light that proceeds from other bodies. Whether their light is transmitted by the actual *emission* of luminous particles, or by the propagation of *undulations* analogous to those of sound, is a question that has been long keenly debated amongst Natural Philosophers; but it is of little consequence to the Physiologist *which* is the true solution, since he is only concerned with the laws according to which the transmission takes place, which are the same on both theories. These laws it may be desirable here briefly to recapitulate.

563. Every point of a luminous body sends off a number of rays, which diverge in every direction, so as to form (as it were) a cone, of which the luminous point is the apex. So long as these rays pass through a medium of the same density, they proceed in straight lines: but if they enter a medium of different density, they are *refracted* or bent—*towards* the perpendicular to the surface at the point at which they enter, if they pass from a rarer into a denser medium—and *from* the perpendicular, when they pass from a denser medium into a rarer. It is easily shown to be a result of this law, that, when parallel rays passing through air fall upon a convex surface of glass, they will be made to converge ; so as to meet at the opposite extremity of the diameter of the circle, of which the curve forms part. If, instead of continuing in the glass, they pass-out again, through a second convex surface, of which the direction is the reverse of the first, they will be made to converge still more, so as to meet in the centre of curvature. Rays which are not parallel, but which are diverging from a focus, are likewise made to converge to a point or focus; but this point will be more distant from the lens, in proportion as the

* This may partly be attributed also to the effluvia adhering to the dress. It has been remarked that *dark* cloths retain these more strongly than *light*. For some sensible observations on the sense of smell in the diagnosis of disease, see D. W. Crompton in the "Birmingham Medical Review," No. viii., Oct. 1873, p. 251, and No. ix. p. 23.

object is nearer to it, and the angle of divergence consequently greater. The rays diverging from the several points of a luminous object, are thus brought to corresponding foci; and the places of all these foci hold exactly the same relation to each other, with that of the points from which the rays diverged; so that a perfect image of the object is formed upon a screen held in the focus of the lens. This image, however, will be inverted; and its size, in proportion to that of the object, will depend upon their respective distances from the lens. If their distances be the same, their size will also be the same; if the object be distant, and the image near, the latter will be much the smaller; and *vice versâ*.

564. There are two circumstances, however, which interfere with the perfection of an image thus formed by a convex lens. The one is, that if the lens constitute a large part of the sphere from which it is taken, the rays which fall near its margin are not brought to a focus at the same point with those which pass through its centre, but at a point nearer the lens. This difference, which must obviously interfere greatly with the distinctness of the image, is termed *Spherical Aberration;* it may be corrected by the combination of two or more lenses, of which the curvatures are calculated to balance one another in such a manner that all the rays shall be brought to the same focus; or by diminishing the aperture of the lens by means of a stop or diaphragm, in such a manner that only the central part of it shall be used. The latter of these methods is the one employed where the diminution in the amount of light transmitted is not attended with inconvenience. The nearer the object is to the lens (and the greater, therefore, the angle of divergence of its rays), the greater will be the spherical aberration, and the more must the aperture of the diaphragm be reduced in order to counteract it.—The other circumstance that interferes with the distinctness of the image, is the unequal refrangibility of the differently-coloured rays which together make up white or colourless light; the violet being more bent from their course than the blue, the blue more than the yellow, and the yellow more than the red; the consequence of which will be, that the violet rays are brought to a focus much nearer to the lens than the blue, and the blue nearer than the red. If a screen be held to receive the image in the focus of any of the rays, the others will make themselves apparent as fringes round its margin. This difference is termed *Chromatic Aberration.* It is corrected in practice, by combining together lenses of different substances, of which the *dispersive* power (that is, the power of separating the coloured rays) differs considerably. This is the case with flint and crown-glass, for instance—the dispersive power of the former being much greater than that of the latter, whilst its refractive power is nearly the same; so that, if a convex lens of crown-glass be united with a concave of flint whose curvature is much less, the dispersion of the rays effected by the former will be entirely counteracted by the latter, which diminishes in part only its refractive power.*

* The most important recent works on the optical relations of the eye, are Helmholtz's "Handbuch der Physiologischen Optik," Leipzig, 1867; and the monographs by Merkel, Waldeyer, Schwalb and others in Gräfe and Sämesch's "Handbuch der Gesammten Augenheilkunde," 1874. MM. Hüppel and Grünhagen have shown ("Archives für Ophthalmol.," Band xiv. p. 219) that the ordinary pressure of the contents of the globe of the eye in the cat is sufficient to support a column of mercury of from 22–24 mm. in height. When the third nerve was irritated, the pressure rose from this average to 70–90 mm., which was apparently due to the contraction of the recti and obliquus inferior. Irritation of the branches supplying the sphincter iridis and ciliary muscle exerted no influence. Excitation of the cervical sympathetic was followed by a primary exaltation and a secondary diminution of pressure. The former effect, amounting to 1–6 mm., was probably due to the contraction of the retractor muscle; the latter appeared to result from contraction of the ocular vessels.

565. The eye commences as a protrusion of the forebrain, the base of the process becoming constricted to form the optic tract, chiasma, and nerve, whilst the peripheral extremity develops into the retina. In front of the retina are various transparent media, partly derived from the mesoblast and partly from the epiblast, the refractive power of which is adapted to form a sharply-defined image of external objects upon the retina. When fully developed, the optic nerves arise by three roots, two white and one grey. The external and larger white root runs to the corpus geniculatum externum, which is in immediate relation with the nates; whilst the internal white root runs into the corpus geniculatum internum, which is connected with the testes. The *external white* root, after entering the posterior part of the thalamus opticus, divides into three fasciculi, one running upwards by the side of the corpus geniculatum externum, to intermingle with the stratum zonale of the optic thalamus; a second enters the pulvinar, or posterior tubercle, after passing beneath the corpus geniculatum externum; whilst the third penetrates the corpus geniculatum externum opposite the optic nerve. The *internal white* root, after penetrating the corpus geniculatum internum, traverses it, and emerging at the opposite side, runs to the *nates*, and perhaps by a few fibres to the testes. The *grey root* may be traced to the grey matter of the third ventricle, which covers the opposed surfaces of the optic thalami. It forms a lamina, which passes obliquely to the upper surface of the optic chiasma. Bellouard* observes that through the stratum zonale of the optic thalamus, and through the inferior root of the thalamus, the optic nerve is brought into relation with the cortex cerebri, the fibres forming the optic radiations of the corona radiata. Through the pulvinar and its optic radiations, it is brought into relation with the cortex of the occipital lobes† and with the medulla by the fibres of the tegmentum of the cerebral peduncle. Other fibres extend from the nates and testes to the cortex cerebri. Collectively these fibres form a projection system of the first order. Stilling‡ also admits an origin from the tuber cinereum and another from the substantia perforata antica.

566. The refractive surfaces of the eye are three in number, and may be regarded as spherical, though the cornea has been shown to be slightly ellipsoidal. The radius of the first refracting surface, which is that of the cornea, is about 7·7 mm.; of the second, which is the anterior surface of the lens, is about 10·3 mm.; and of the third, which is the posterior surface of the lens, about 6·1 mm. The distances between these are: from the anterior surface of the cornea to the anterior surface of the lens varies from 2·0 to 3·1 mm.; the distance from the anterior surface of the cornea to the posterior surface of the lens, from 7·1–7·5 mm. The thickness of the lens therefore varies from 4 to 4·6 mm. The distance from the posterior surface of the lens (Knapp) to the retina is about 14 mm. The total length of the optic axis is 22·0 mm. The index of refraction is for the cornea 1·377, for the lens 1·45, vitreous humour 1·3366, and for the aqueous 1·377. In order that the course of a ray of light may be followed in any system of refractive media, it is necessary that the position of the five cardinal points should be known—namely, that of the *two principal points*, which are the points where the principal refracting surfaces are cut by the axis; that of the *two nodal points*, or those points in the refractive media to which a ray of

Monniki ("Tonometers en Tonometrie," Inaug. Dissert., Abst. in "Syd. Soc. Year Book," 1871–72, p. 339) ascertained that the tension of the eye varied within rather wide limits. It is normal when a pressure of 150–225 grains produces a depression of ¼ of a millimeter.

* "De l'Hemianopsie," 1880, p. 15.

† See also Munk, "Verhand. d. Phys. Gesells. zu Berlin," Sitzng. 4 July, 1879.

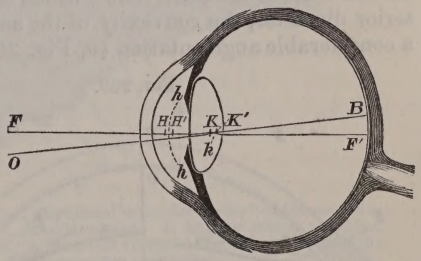
‡ "Centralblatt f. prakt. Heilkunde," Band iv. 1880, p. 40.

light is directed before, and appears to proceed from, after its refraction; and lastly, of the *focal*, or rather of the *two focal points*, one behind the lens and the other in front of the cornea. The relative positions of these cardinal points are as follows:—

1. Principal point, 2·1746 mm. behind the anterior surface of the cornea.
2. Principal point, 2·5724 „ „ „ „ „
1. Nodal point, 0·7850 „ in front of the posterior surface of the lens.
2. Nodal point, 0·3602 „ „ „ „ „
2. Focal point, 14·6470 „ behind „ „ „
1. Focal point, 12·8326 „ in front of the anterior corneal surface.

The two principal points thus lie at 0·4 mm. distance from one another, nearly in the middle of the anterior chamber of the eye. The two nodal points, also about 0·4 mm. from each other in the posterior part of lens; the second focal point for parallel rays close to or in the retina. The two nodal points lie so close to one another that they may be regarded as single, and visual rays passing through them as rectilinear. In like manner, the two principal surfaces may be regarded as marked in the spherical surface *h h*, which represents the refractive surface of the eye. Every point of a retinal image corresponds to a point of the object; and if it be desired to determine which are the corresponding points of the object and of the image, it is only requisite to join them by a line passing through the united nodal point. The retinal images are consequently inverted.

Fig. 259.

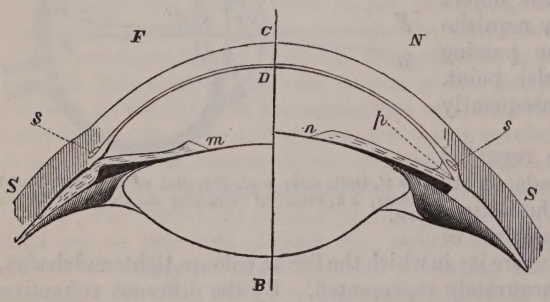


F F', Optic axis; H H', Principal points; K K', Nodal points; *h h*, Principal refracting surface; O B, Visual axis.

567. The Eye may be regarded as an optical instrument adapted to produce, on the surface of the Retina, a complete image or picture of luminous objects brought before it; in which the forms, colours, lights and shades, &c., of objects are all accurately represented. By the different refractive powers of the transparent media through which the rays of light pass, and by the curvatures given to their respective surfaces, both the Spherical and Chromatic aberrations are corrected in a degree sufficient for all practical purposes; so that, in a well-formed eye, the picture is quite free from haziness and from false colours. The power by which the eye adapts itself to variations in the distance of the object,—so as to form a distinct image of it, whether it be six inches, six yards, or six miles off,—is extremely remarkable, and has only recently been completely explained. It is obvious that, if we fix upon any distance such as that for which the eye is naturally adjusted (say 12 or 14 inches, the distance at which we ordinarily read), the rays proceeding from an object placed nearer to the eye than this would not be brought to a focus upon the retina, but would converge towards a point behind it; whilst, on the contrary, the rays from an object at a greater distance would meet before they reach the retina, and after crossing would have again diverged from each other when they impinge upon it; so that, in either case, vision would be indistinct. Now, two methods of adaptation suggest themselves to the Optician. Either he may vary the distance between the refracting surface and the screen on which the image is formed, in such a manner that the latter shall always be in the focus of the converging rays;

or, the distance of the screen remaining the same, he may vary the convexity of his lens, in such a manner as to adapt it to the distance of the object.* It has been thought that a change in the position of the retina might be effected by the recti muscles pressing upon the globe, and thus rendering its antero-posterior axis longer; but the power of accommodation may still be preserved when these muscles are paralyzed, whilst the entire loss of the power of adapting the Eye for different distances, which is experienced after the removal of the crystalline lens in the operation for cataract, or in cases of the congenital absence of this body, shows that some change in its place or figure is the principal means whereby the ordinary adaptation is effected. The precise changes which occur in the interior of the Eye when it is accommodated for viewing near objects, or during *positive accommodation*, have been determined by Helmholtz† with an instrument that he has termed an Ophthalmometer, the principle of which consists in examining the reflexion from the various ocular media of two flames:—alterations in the relative position and figure of which can be readily perceived and measured and furnish the data for the requisite calculations. By this means it has been ascertained that the essential alteration in the lens is a change effected in its figure by a muscular effort under the influence of the third nerve which increases its thickness in the antero-posterior diameter, the convexity of the anterior surface in particular undergoing a considerable augmentation (*n*, Fig. 260), and advancing towards the cornea; whilst the convexity of the posterior surface is but slightly augmented, and undergoes scarcely any change of place. The other and clearly secondary changes which have been observed are a contraction of the circular fibres of the Iris, making the pupil smaller—the pupillary edge of the Iris at the same time moving forwards, and the attached or peripheral edge (*p*) backward. The forward movement of the plane of the Iris amounts, according to Knapp,‡ to about 1-12th of an inch. Lastly, according to Becker,§ the points of the ciliary processes retire from the edge of the lens. The return of the lens to

Fig. 260.



C, Cornea; S, Sclerotic; F C N, Vertical plane of the Cornea; B C D, Axis of the Eye; *s s*, Canal of Schlemm; *p*, Angle formed by the Iris and Cornea, or margin of anterior Chamber; *m*, Position of Iris, and curvature of Lens in an Eye converged for parallel rays, distant vision, or negative accommodation; *n*, Position of Iris, and curvature of lens required for near objects, or for positive accommodation.

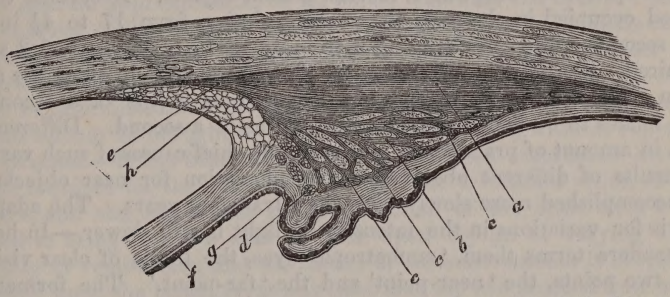
* According to the calculations of Olbers, based on the ascertained refractive powers of the media of the eye, the difference between the focal distances of the images of two objects, the one so far off that its rays are parallel, and the other at the distance of only four inches from the eye, is about 0·143, or one-seventh of an inch; but as the usual range of distinct vision does not extend to objects brought within six or seven inches, the amount of change required in the relative places of the refracting bodies and the retina would not ordinarily exceed a line.

† A full confirmation of Helmholtz's statement, with a good historical *résumé* of the whole subject, will be found in Gräfe and Sämesch's "Handbuch der gesammten Augenheilkunde," 1874–75. ‡ "Archiv f. Ophthalmol.," Band vi. Abtheil. ii. p. 1.

§ See his interesting Paper in Braun, Duchek, and Schlager's "Medizin. Jahrb.," 1864, p. 1. Coccius, in "Der Mechanismus des Menschlich. Auges," Leipzig, 1868, on the other hand, states that in accommodation for near objects as observed in eyes that have been operated on for iridectomy, the ciliary processes advance and swell up.

its original figure, after the cessation of the effort by which it has been accommodated for the distinct vision of near objects, is effected by the relaxation of the ciliary muscle, which permits the elasticity of the suspensory ligament to come into play. Under these circumstances the lens (*m*) becomes flattened, the peripheral margin of the iris is brought forward, the pupil dilates under the influence of the dilatator pupillæ, which is innervated by the Sympathetic nerve, the tips of the ciliary processes are approximated to the margin of the lens, and the so-called *negative accommodation* is effected. The main instrument in effecting these changes in the Eye appears to be the *Ciliary Muscle*, the structure and attachments of which were first clearly described by Mr. Bowman. It consists of unstriped muscular fibre, partly arranged in a circular manner, the innermost fibres (sometimes termed Müller's muscle) running parallel to the margin of the Cornea (*d*, Fig. 261), and partly dis-

Fig. 261.



Section of the Ciliary Region of the Eye in Man. *a*. Meridianal muscular fasciculi of the musculus ciliaris. *b*. Deeper seated radiating fasciculi. *c c c*. Annular plexus. *d*. Annular muscle of Müller. *f*. Muscular lamina on the posterior surface of Iris. *g*. Muscular plexus at the ciliary border of the Iris. *e*. Annular tendon of the musculus ciliaris. *h*. Ligamentum pectinatum.

posed radially (*a*), the fibres of the latter portion of the muscle appearing to be connected at their origin with the posterior elastic lamina of the Cornea, and externally or posteriorly being partly inserted into the Iris, forming the pillars of the Iris (Ligamentum pectinatum iridis), partly into the Sclerotic bounding the canal of Schlemm (*s*, Fig. 260), and partly and chiefly into that part of the outer surface of the choroid tunic, which corresponds to the ciliary processes. The movement which effects the change of form of the crystalline lens is performed in obedience to Volition, and is guided by sensation; yet we are not conscious of performing it, all that we *will* being the *result*: and thus we have another apposite illustration of the really automatic nature of what are termed 'voluntary movements' generally. The reasons for believing that the Eye, or rather the ciliary muscle, is passive in accommodation for distance are—the absence of any feeling of effort in persistently looking at a distant object, whilst a sense of effort and fatigue are soon experienced in looking at objects closely approximated to the Eye; the fact that the Eyes, on being opened after long closure, are adapted for distance; the impairment or absolute loss of the power of the accommodation in cases of paralysis of the Third nerve, by which the ciliary muscle is innervated, or when the muscle has been paralysed by Atropine. The object fulfilled by the contraction of the pupil in adaptation of the Eye for near objects, is evidently to exclude the outer rays of the cone or pencil, which, from the large angle of their divergence, would fall so obliquely on the convex surface of the eye as to be much affected by the spherical aberration, and thus to allow the central rays only to enter the eye, so as to secure the sharp definition of the

image; the principle being exactly the same as that on which the optician applies a *stop* behind his lenses, which reduces their aperture in proportion to the shortness of their focal distance. The channel through which this action is effected is evidently the same as that through which the convergence of the eyes is produced—namely, the inferior branch of the Third pair of nerves; to the action of which, the sensations received through the retina seem to afford the immediate stimulus, in the same manner as they do to the ordinary variation in the diameter of the pupil under the influence of light; but the voluntary determination to fix the vision upon the object is the original source of the action. That the presence of the Iris is not indispensable for the performance of positive accommodation is shown by the fact that, in a patient from whom Gräfe removed the whole Iris, this faculty remained perfect; and a similar power has been observed to exist in cases of congenital absence of the Iris.* The time occupied in accommodating the Eye for near objects is greater than that required for adapting it to view distant objects. According to Aeby the period occupied in changing the accommodation from 17 to $4\frac{1}{2}$ inches is about 2 seconds, whilst in changing it from $4\frac{1}{2}$ to 17 inches only 1·2 seconds are required. Vierordt, however,† states that he was able to effect the accommodation from 60 feet to $4\frac{1}{2}$ inches in about nine-tenths of a second, and from $4\frac{1}{2}$ inches to 60 feet in about seven-tenths of a second. Differences in age, and in amount of practice, are probably the chief causes of such variations in the results of different observers; accommodation for near objects being always accomplished more slowly with the advance of years. The adaptation of the Iris for variations in the intensity of light is still slower.—In healthy, or, as Donders terms them, 'emmetropic' eyes, the limits of clear vision lie between two points, the 'near-point' and the 'far-point.' The former, very near the eye in infancy, gradually recedes with advancing age; and Fellenberg‡ has shown, that at 10 years of age it is $2\frac{2}{3}$ inches distant from the front of the cornea; at 20 years of age, $3\frac{5}{9}$ in.; at 30, $4\frac{4}{5}$ in.; at 40, $6\frac{6}{7}$ in.; at 50, 12 in.; at 60, 24 in.; and at 70, 144 inches. The 'far-point' for healthy eyes is infinite distance, or, in other words, the refractive media of healthy eyes in a condition of repose are adapted to bring parallel rays to a focus on the retina. The field, or extent of the range of vision for each eye is very considerable.§ Measured from the optic papilla as a centre, it was found by Förster to be upwards 45°, downwards 65°, outwards 70°, and inwards 60°.

* See Dr. Soelberg Wells' instructive paper 'On the Paralysis of the Muscles of the Eye,' in the "Ophthalmic Hospital Reports," vol. ii. 1859–1860, p. 199.

† Henle and Meissner's "Bericht," 1857, p. 547.

‡ Canstatt's "Jahresbericht" for 1862, p. 157.

§ Landolt ('Il perimetro e la sua applicazione,' Quaglino's "Annal. d'Ottalmologia," Gennajo, 1872) gives rather higher numbers—viz., 135° for the horizontal and 120° for the vertical arc; and Uschakoff (Reichert and Du Bois-Reymond, "Archiv," 1870, p. 454) and Reich (Gräfe and Sämesch, "Handb. der Augenheilkunde," Band iii. 1874, p. 59) higher still—namely, in the horizontal meridian, max. 142°, min. 137°; and in the vertical, max. 120°, min. 114°. The field of vision is smaller in myopes and rather larger in hypermetropes than in healthy or emmetropic eyes. Helmholtz gives as average numbers derived from his observations the following values to the varying optical constant and cardinal points. The numbers, where not otherwise expressed, represent the distance from the anterior surface of the cornea in millimetres:—

	In accomodation For distance.	For near objects.
Radius of curvature of cornea	8	8
Radius of curvature of anterior surface of lens	10	6
Radius of curvature of posterior surface of lens	6	5·5
Situation of anterior surface of lens	3·6	3·2
„ of posterior	7·2	7·2
Focal distance of lens	43·707	33·785

Landolt found it to be upwards 55°, downwards 65°, outwards 85°, and inwards 50°.* The blind spot corresponding to the entrance of the optic nerve extends from 12°–18° along the horizontal plane of the retina. The actual rotation of the globe, or as Schuurman† terms it, the mean excursion of a healthy or emmetropic eye from the central point is inwards 45°, outwards 42°, upwards 34°, and downwards 57°.

568. When both eyes are fixed upon an object, their axes converge so as to meet in it; and the degree of convergence is of course altered by variations in the distance of the object; since, when the object is very remote, the optic axes are virtually parallel, whilst its approach causes them to incline towards each other, and this the more rapidly as the object is brought nearer, the increase being the greatest when it has arrived within the ordinary distance of distinct vision. Here, again, we have an example of the automatic nature of voluntary actions; for the convergence of the eyes that may be produced by this gradual approximation of an object on which the eyes are kept fixed by an exercise of the Will, far exceeds that which most individuals can induce by an effort made directly for the purpose; and if, when an object has thus been gradually approximated to within a few inches of the nose, the voluntary fixation be intermitted, and the optic axes be allowed to regain their parallelism, they can seldom be brought to converge again upon it, without repeating the whole process.—It has been thought, from the close accordance between the changes required for the adaptation of the eyes to distinct vision at different distances, and the alterations in the direction of the optic axes which are required to bring the two eyes to bear upon objects at varying degrees of proximity or remoteness, that the former of these movements is in some degree dependent upon the latter, or, at any rate, that the two proceed from a common motor impulse. But that the convergence of the axes is not itself in any way the occasion of the alteration of the focus of the eye, is shown by these two facts; first, that the adaptation is as perfect in a person who only possesses or uses one eye, as it is when both are employed; and second, that some persons possess the power of altering the focus of the eyes by an effort of the will, whilst the convergence remains the same.

569. The ordinary forms of defective vision, which are known under the names of *Myopia* and *Hypermetropia*, or 'short-sightedness' and 'long-sightedness,' are entirely attributable to defects in the optical adaptation of the eye. As already stated, the healthy, or *emmetropic* Eye, when at perfect rest is adapted to focus parallel rays on the retina (A, Fig. 262). If, however, a near object be looked at, since the rays proceeding from it are divergent, it is obvious that without some change in the media the image, instead of being focussed on the retina, would be focussed behind it. The Eye, by its power of accommodation, due to the action of the ciliary muscle in causing the lens to become thicker, is capable of effecting this alteration; and it is by an effort that increases with the proximity of the object that all near objects

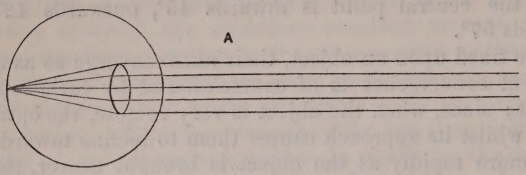
	In accommodation For distance.		For near objects.
Posterior focal distance of the eye	19·875	...	17·756
Anterior focal distance of the eye	14·858	...	13·274
Position of anterior focal point	12·918	...	11·241
Position of first chief point	1·9403	...	2·0330
Position of second chief point	2·3563	...	2·4919
Position of first nodal point	6·957	...	6·515
,, second	7·373	...	6·974
,, posterior focal point	22·231	...	20·248

* Pufahl, "Archiv f. Augen und Ohrenheilkunde," 1878, p. 25.

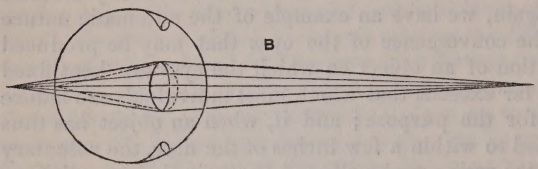
† Gräfe and Sämesch, "Handbuch d. ges. Augenheilkunde," Band iii. p. 233, 1874.

are seen. In Hypermetropia (c), or long-sightedness, either the Eye as a whole is flattened from before backwards, or the lens is too flat, or both conditions may be present together. In either case, even *parallel* rays are not brought to a focus on the retina, much less divergent rays, such as those coming from near objects. It requires, in fact, muscular effort to bring parallel rays to a focus on the retina, and a very great effort, which cannot long be maintained, to bring divergent rays. The patient consequently complains of pain after a few minutes' reading or writing. To remedy this state, the eyes are placed in a passive state by the instillation of atropia; the strongest glass is then given, which produces distinct vision of distant objects (objects at 20 feet or more), or, in other words, which will focus parallel rays on the retina. In Myopia (D) either the Eye is too long in the antero-posterior direction, or the lens is too thick, or both conditions concur, and parallel rays, striking the cornea, are brought to a focus in front of the retina, and, after decussating, form a circle of dispersion on this membrane. All distant objects, therefore, are seen obscurely. On the other hand, the patient can see objects close to his eye, because the rays are there highly divergent. This condition may be remedied by placing a concave lens in front of the eye, which causes the rays of light to become divergent, and they are not therefore brought to a focus so soon in the interior of the eye. An interesting experiment, capable of a practical application in determining whether a given eye is normal or ametropic, and whether the ametropia is myopic or hypermetropic, is that known as Scheiner's experiment (Fig. 264); in this, a card or thin piece of metal, perforated with two small holes, the distance between which must be less than the diameter of the pupil, is placed before the eye. If the eyes be n ormal, two circles of light will be seen, which overlap one another to a cert ain extent, and in this brighter part all objects appear single, because the rays are united upon the retina at *c*. If, however, the axis of the eye be too long, as in Myopia, and the retina be at *p q*, the rays will have crossed, and double im ages will be seen in the central part of the field of vision; whilst if

Fig. 262.

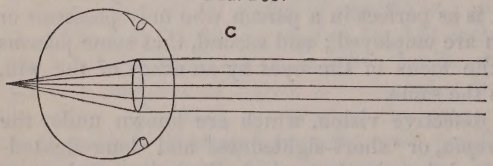


Emmetropic Eye. Parallel rays focussed on the retina.

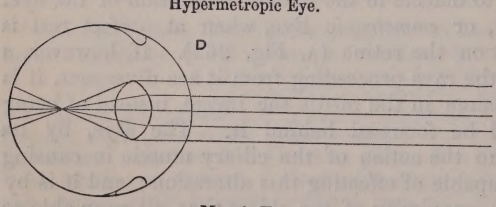


Emmetropic Eye. The dotted lines showing how accommodation for the diverging rays of near objects is effected.

Fig. 263.



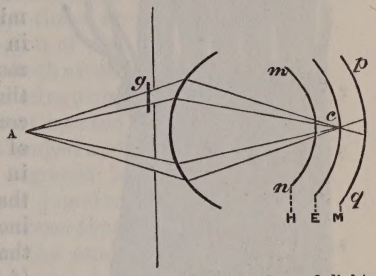
Hypermetropic Eye.



Myopic Eye.

the axis of the eye be too short, as in Hypermetropia, the rays will not have united, and double images will also be seen. By placing a piece of red or green glass over one of the holes, as at *g*, it is easy to determine whether the ray passing through that hole has or has not crossed* The term 'presbyopia,' as limited by Donders, simply expresses a deficient power of accommodation in the eye, resulting from increased density of the lens, or from defective power of the ciliary muscle, so that the 'near point' recedes beyond a certain point, arbitrarily fixed by Donders for the sake of convenience at eight inches. The effects of Atropine of Duboisia upon the eye are very remarkable, not only in dilating the pupil to the utmost in the course of from twenty to twenty-five minutes, but in completely paralyzing the ciliary muscle, and with it the power of accommodation, so that the 'near point' becomes gradually more and more distant, till at length it coincides with the 'far point.' Eserine, the active principle of the Calabar bean, on the contrary, causes extreme contraction of the pupil in the course of a few minutes, the 'far point,' and in many eyes the 'near point' also, becoming approximated to the eye, though the power of accommodation is never altogether lost. Both of these agents appear to exert a stimulating as well as a paralyzing influence on the nerves supplied to the Iris; atropine paralyzing the third and exciting the sympathetic nerve, whilst the Calabar bean paralyzes the sympathetic and excites the third.† The term *Astigmatism*‡ (*a*, privative, and *στίγμα*, a point) has been applied by Professor Whewell to a condition of the eye (first observed in himself by Professor Airy) in which there is an inequality in the refractive power (owing to difference in the degree of curvature either of the cornea, or of the lens, or of both) between the horizontal and vertical meridians of the eye. There is a consequent incapacity on the part of the eye to collect all the rays of light entering it to one exact focus; this has been shown by Donders to be of common occurrence in those who are otherwise healthy. A very slight degree of astigmatism is indeed natural since the cornea has been shown to be the top segment of an ellipsoid with three unequal axes. The asymmetry in disease is usually of such a nature that with each degree of accommodation horizontal lines are seen distinctly at a point nearer to the eye than vertical lines, showing that the vertical meridian has a shorter focal distance than the horizontal. This condition may be remedied by the use of the so-called cylindrical glasses. Many other interesting inquiries, respecting the action of the eye as an optical instrument, suggest themselves to the Physical philosopher; but the foregoing are the chief in which the Physiologist is concerned; and we shall now proceed, therefore, to consider the share which the nervous apparatus performs in the phenomena of vision.

FIG. 264.



Scheiner's Experiment. A, source of light; E, position of retina in regard to the focus C of the rays entering through two apertures in a card, one of which is covered with a coloured glass *g* in an emmetropic eye; H, position of the retina *m n* in an hypermetropic eye; M, position of retina *p q* in a myopic eye.

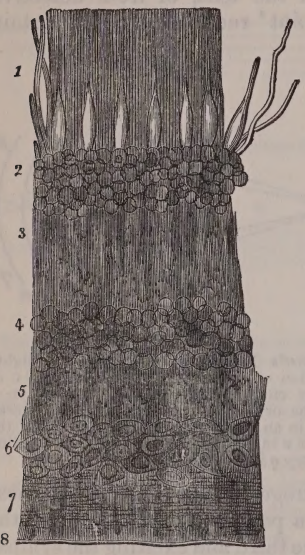
* See Thompson, "Amer. Journ. Med. Sci.," April, 1870.

† See the Essays of Rogow, in Henle and Pfeuffer's "Zeitschrift," Band xxix. 1867, p. 1; Bernstein in idem, p. 35; Dr. Argyll Robertson on Calabar Bean, "Trans. of Royal Soc. of Edin.," vol. xxiv.; V. Gräfe, "Archiv f. Ophth.," Band ix. Heft iii. p. 87.

‡ See Donders' "Astigmatismus," &c. (Berlin, 1862); the "Oration" delivered by Mr. Z. Laurence before the North London Medical Society, 1863, and his papers in the "Med. Times and Gazette" for 1862–63.

570. The Optic Nerve,* at its entrance into the eye, divides itself into numerous small fasciculi of ultimate fibrils; and these appear to spread themselves out, and to inosculate with each other by an exchange of fibrils, so as to form a net-like plexus which constitutes the inner layer of the Retina (Fig. 265, 7) in immediate contact with the 'limitary membrane' (8). There is considerable difficulty, however, in the precise determination of the course of the nerve-fibres in the Retina, on account of their minute size, their softness, and the alteration in their characters that takes place during mounting. Although uniformly much smaller than ordinary nerve-fibres, they present considerable diversities in size, the largest of them being only about 1-6000th of an inch in diameter, whilst the smallest are no more than from 1-30,000th to 1-50,000th of an inch. It is considered by Mr. Bowman that, like the fibres of the Olfactory nerves (§ 560), they consist of axis-cylinders without sheaths. They do not form a continuous layer at the yellow spot. Externally to the stratum of nerve-fibres, which may be called the Optic layer, is a vesicular stratum, called the ganglionic layer (Fig. 266, 3), which consists of a finely-granular matrix, wherein are imbedded nerve-cells resembling those of the nerve centres, and having, like them, one, two, or a variable number of processes, some of which appear to become continuous with the fibres about to be described; at the macula lutea all the ganglion cells are bipolar.

Fig. 265.



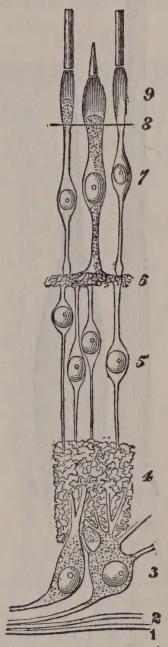
Vertical Section of *Retina* of the Human Eye:—1, bacillar layer; 2, outer granular layer; 3, intermediate fibrous layer; 4, inner granular layer; 5, finely-granular grey layer; 6, layer of nerve-cells; 7, layer of fibres of optic nerve; 8, limitary membrane.

It is to these fibrous and vesicular layers of the Retina, which together make-up the analogue of the cortical substance of the Cerebrum, that the principal supply of blood is distributed, by the minute capillary network which is spread-out through their substance. Immediately external to the ganglionic layer is the internal molecular layer (4) or the layer of grey vesicular matter of Mr. Bowman, the peculiar appearance of which is due to the admixture of a very fine plexus of spongy connective tissue given off from certain radially running supporting fibres, with nerve-fibrils of immeasurable minuteness. This again is succeeded by the layer of inner granules (5), which contains two distinct kinds of nucleated cellular elements, one of which is imbedded in radially arranged nerve-fibres, and the other in similarly disposed fibres of connective tissue; next comes (6), the external molecular or granulated layer, consisting of a thin layer of fine plexiform tissue, enclosing a few nuclei and smooth cells, with coarser fibres running parallel to the surface of the retina. The external granule layer (7), which consists of a thin layer of granules, lying in a finely striated matrix of connective tissue, in which extraordinarily fine fibrils are imbedded, running obliquely or parallel to the surface of the retina, and attached to the peripheric processes of the internal

* An excellent account of the historical development of our knowledge of the structure of the retina, from the year 1856 to the year 1868, is given by Krauss, in "Robin's Journal," Band vi. 1869, p. 438.

granules, and to the fibres of the rods and cones; and finally the layer of rods and cones (9), often also called the bacillary layer, or after its discoverer, Jacob's membrane. The rods are cylindrical bodies, with a length at the back of the Eye in Man of fifty to sixty micro-millimeters, and a diameter of two micro-millimeters, but becoming shorter anteriorly. Distributed at regular intervals between the rods, except at the macula lutea and ora serrata, are the flask-shaped cones. The distance between two cones amounts on an average to eight or ten micro-millimeters, the intervening space being occupied by three or four rods in a straight line, but in the region of the fovea centralis the distance is much less. In both structures two essentially different segments are distinguishable. (See Fig. 267.) The distinction is most marked in the cones, in which the outer segment is conical and highly refractile, whilst in the rods the segment is usually regularly cylindrical. The plane of junction of the two segments is more anterior in the cones than in the rods. After removal from the body the outer segments of both the rods and cones undergo a kind of coagulation, imbibe water, yield myelin drops, and break up into a series of disks, or become distorted. When well preserved they exhibit a longitudinal and very fine striation. Ritter, and others, think that an axial fibre can be seen in the *outer* segment of the rods. The internal segments of both rods and cones exhibit a fine longitudinal striation on their surface, which are rather channellings or fibres, probably the latter, since they both surround the base of the inner segment, and protrude from its outer extremity, enclosing the base of the outer segment in a kind of cradle. Hensen and some others believe that an axial fibre may be seen in the *internal* segment of the rods in some animals, but such fibres are not visible in man. The nucleated cone granule is a bipolar cell, the peripheric process of which is the cone itself, whilst the central extremity arises from the external molecular layer, by the coalescence of a number of fine fibrils. The rods and cones, the latter of which present in many animals, as in birds and reptiles, a drop of brilliant-coloured oily substance at their peripheric extremities, are the terminal organs of the optic nerve-fibres; but it still remains undecided whether the fibrils in the interior of the inner segment stand in connection with the nerve-fibrils of the fibres in question. The outer segment may possibly represent a non-nervous physical accessory apparatus. It is remarkable that section of the optic nerve in the living animal is followed by degeneration of all the elements of the retina except the bacillary layer, which thus scarcely seems to belong to the true nerve tissues. The layer of hexagonal pigment cells, commonly termed the pigment epithelium of the choroid, belongs both physiologically and morphologically to the retina. The outer segments of the rods and cones are so closely embraced by them, in well-preserved specimens, that they will rather separate from the internal segments or fracture through their substance than become detached from

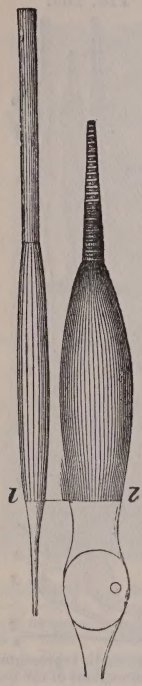
Fig. 266.



Diagrammatic representation of the connections of the nerve-fibres in the Retina. 1. Membrana limitans interna. 2. Optic nerve-fibre layer. 3. Layer of ganglion cells. 4. Internal granulated or molecular layer. 5. Internal granule layer. 6. External granulated or molecular layer. 7. External granule layer. 8. Membrana limitans exterior. 9. Bacillary layer, or layer of rods and cones.

them. The proper nervous structures of the retina are permeated and supported by a stroma of connective tissue, which is bounded externally and internally by the membranæ limitantes, the external limiting membrane corresponding to the inner extremity of the rods and cones or line of detachment of Jacob's membrane; and the internal limiting membrane (8, Fig. 265) resting on the hyaloid. The *supporting connective tissue* (Fig. 268) is closely allied structurally to that of the brain and spinal cord, which has been named Neuroglia by Virchow. By Schultze it is termed spongy connective tissue. It fills up the interspaces between the ganglion cells, granules, and nerve-fibres, and consists of radial supporting fibres (most constantly found in the internal granule layer) and oval homogeneous nuclei.

Fig. 267.



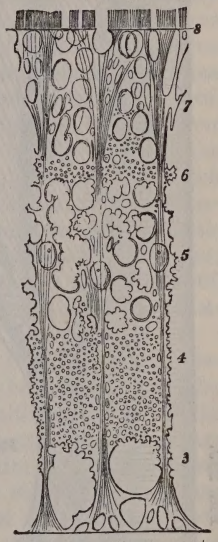
Rod and cone from the Retina of Man preserved in a two per cent. solution of perosmic acid, to show the fine fibres of the surface, and the different lengths of the internal segment. The outer segment of the cone is broken up into disks, which, however, are still adherent to one another; at the base of the cone are seen a few fine hairs; *l*, limiting membrane (×1000 diam.).

571. *Vision or Visual Purple. Rhodopsin.*—The outer segment of the rods of the retina is characterized by the presence of colouring matter, which from its tint is termed "visual purple," or Rhodopsin. It appears to be very generally present, Kühne having only noticed its absence in the Bat, in some Birds, and in Reptiles. The outer segments of the cones are uncoloured; and in the case of the rods, it is remarkable that the colour is absent in those that are near the fovea centralis and in those which are near the ora serrata. The colouring matter is developed before birth. It dissolves readily in a solution of the biliary acids, and especially in purified colourless ox-bile. The solution on exposure to light rapidly bleaches, changing from carmine to red and yellow (chamois), and then becoming colourless and transparent as water. Under spectroscopic examination, visual purple is found to absorb all the rays of the spectrum, from the yellow-green to the violet; whilst it allows a little violet, much of the yellow, and all the orange and red to traverse it. A rosy retina becomes quite pale in the course of fifteen minutes when exposed to the yellow-green portion of the spectrum; more slowly in the blue-green, blue, indigo, and violet; whilst it scarcely undergoes any change in the red and ultra violet. The colour fades even in the living animal on exposure to light, and with rapidity proportionate to the intensity of the light; hence, the rosiest retinæ are obtained from animals which have been kept for some time in the dark, and in order to preserve the colour for experimental purposes, it is requisite to perform all requisite manifestations by the monochromatic sodium light. Other agents which rapidly induce bleaching of the colour are—almost all acids, ether, alcohol, chloroform, turpentine, chlorine, iodine, and bromine. A temperature of 76° C. (169° F.) destroys the colour of the retina of the frog

* The existence of this colouring matter was known as long ago as 1839, when it was noticed by Krohn in the eyes of Cephalopods. Leydig and Schultze subsequently found that the eyes of Arthropods also possessed a rose-coloured pigment. In 1851, H. Müller stated that the rods of the retina of the frog were red, and his observations have been corroborated by Leydig, Boll, and Kühne. See the "Photo-chemistry" of Kühne, translated by Mrs. Foster, 1878; and Kühne's article on the "Chemistry of the Retina," in Hermann's "Handbuch der Physiologie 'Der Sinnesorgane,'" p. 259.

almost instantaneously; of 65° C. (149° F.) in half an hour; whilst at 50° C. (122° F.) it long remains unaltered. It is not acted on by ammonia, common salt, alum, iron and zinc sulphate, ozone, oils, urea, or by trypsin digestion. Alum acts as a mordant, and prevents the colour from undergoing further change by the action of light. By throwing upon the retina of an animal that has been for some time kept in the dark the well-defined image of a brightly illuminated object for a short period, the part on which the light falls is bleached, whilst the remaining portion retains its colour; and when this is fixed by a solution of alum, an "*optogram*" may be obtained, in which the details of the illuminated object may be recognized. It would appear from this that during life the retinæ, when exposed to light, are constantly being bleached, the colouring matter undergoing a constant renewal; but the absence of the rhodopsin in the neighbourhood of the fovea centralis, which is the most sensitive part of the Eye for form, size, and colour, forbids the supposition that it is of great importance in ordinary visual perception. The *internal* segments of the cones of birds and reptiles contain coloured fat globules, and Kühne has applied the term "chromophane" to the colouring matter they contain.

Fig. 268.



Diagrammatic representation of the connective tissue of the retina as seen near the ora serrata. The numbers correspond to those of the several layers of the retina given on p. 729.

572. It has been observed that the retinæ of frogs which have been exposed to the light separate with more difficulty from the choroid than those of frogs which have been kept in the dark, whilst at the same time the pigmented epithelial layer is more strongly adherent to the rods. This difference in the relations of the retina* has been shown to be due to a change in the position of the pigment, or "Fuscin needles" of Kühne, and to a movement of the protoplasm. In the eyes of frogs retained in the dark, the pigment is concentrated in the body of the cell, a small quantity only lying between the rods and extending for about one-third the length of the outer limbs. But after exposure to light, the pigment is found to a very large extent arranged in strata between the rods. Hence it would appear that light acts as a stimulus to the cells of the retinal epithelium, which are excited by it to throw out pseudopodic processes, which pass down between the outer limbs of the rods. In darkness the processes are retracted. Red light appears to act as a still more powerful stimulus than white. The adhesion of the epithelium to the rods is augmented by a low temperature, whilst it is diminished by the action of curare. The effect of the phototropic stimulation of the retina has been carefully worked out by Kühne.

573. There are two spots in the Retina in which the arrangement of the foregoing components is essentially different from the rest, and from these differences important physiological conclusions may be drawn. One of these is the slight eminence at which the Optic nerve enters, which is a little below and internal-to the posterior extremity of the axis of the eye. The other is the 'yellow spot of Soemmering,' which is situated in the exact centre of the retina. The modifications undergone by the Retina at the macula lutea

* See Boll, "Monatsbericht d. Berlin Acad.," January and February, 1877; Czerny, "Sitzs.-ber. der Wien. Acad.," Band lvi.; and Kühne in Hermann's "Handbuch der Physiologie," Band vii. 1879, p. 333.

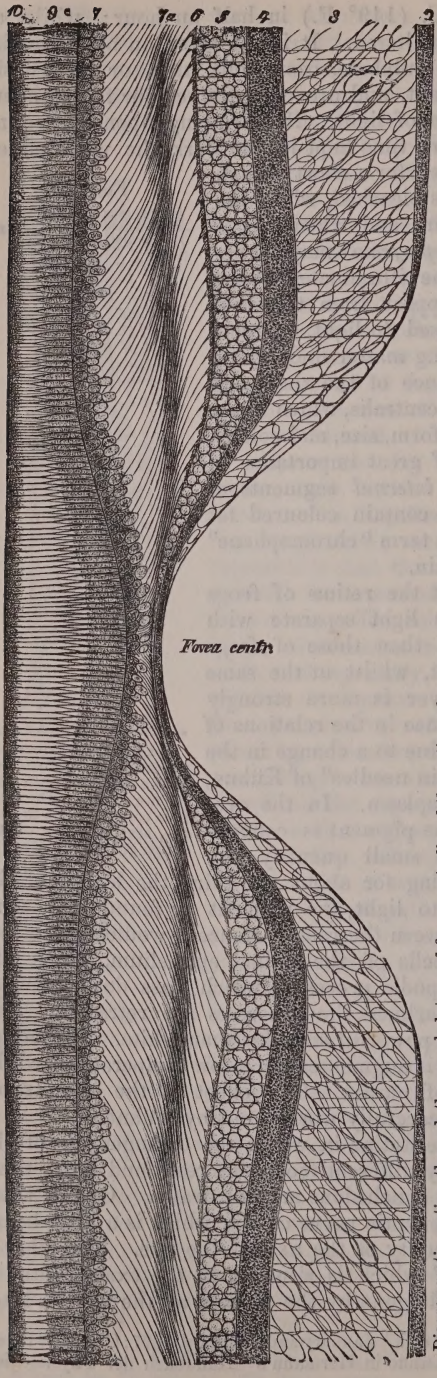


Fig. 269.

Diagrammatic section through the macula lutea and fovea centralis of the retina of man. 2. Optic nerve fibres. 3. Ganglion cells. 4. Internal granular (molecular) layer. 5. Internal granule layer. 6. External granular (molecular) layer. 7 *a*. External fibrous layer. 7. External granule layer. 9. Rods and cones. 10. Pigment layer.

and fovea centralis are considerable. Nearly in the axis of vision an intensely yellow pigment is deposited between the elements of the different layers, with the exception of the bacillar and external granular layer. The centre of the yellow spot is depressed anteriorly (Fig. 269) to form the fovea centralis. The retina is thicker at the macula lutea, of course excepting at the fovea centralis, than in the adjoining parts, and is at the same time softer and more prone to post-mortem change, probably in consequence of the deficiency of the radial supporting connective tissue. The layer of the ganglion cells and internal division of the external granule layer, are the layers that are most obviously thickened. On the other hand, there is no continuous layer of nerve-fibres beneath the membrane limitans interna. The rods are altogether deficient, their place being taken by the cones, which become longer and narrower, and are closely packed, about 135 being contained in the 1-100th part of a square millimeter. The course pursued by the cone-fibres changes as compared with other parts of the retina from a radial to a horizontal direction. At the fovea all the layers of the retina, with the exception of the cones and external granules, diminish to a minimum. Krause estimates the number of the fibres in the optic nerves at one million, the number of the cones at seven millions, and of the rods at 130 millions.* More re-

* Krause, "Allgem. u. Mic. Anat.," 1876.

cently Salzer* finds the number of optic nerve fibres to be 438,000, and of cones 3,360,000, or from seven to eight cones for each nerve-fibre.† And hence it seems unequivocally to follow, that visual impressions cannot act primarily upon the nerve-fibres ;—a conclusion which harmonizes with the fact, that the fibres of the optic nerve are superimposed upon each other in the stratum which they form, in such numbers that it is not conceivable that they should be the primary recipients of luminous impressions, since their transparency must allow rays of light to penetrate from one portion of the layer to another. The bacillary layer was formerly regarded as a reflecting apparatus, having for its purpose to stop the further passage of light, and to intensify its influence on the true retina; but since its connection with the proper nervous elements of the retina has been established, there seems much ground for believing (with Prof. Kölliker) that its rods and cones are the primary recipients of luminous impressions, and that they communicate their condition to the fibres of the optic nerve, by means of their own delicate fibrous prolongations, which seem to come into more or less direct connection with its ultimate ramifications. It is not a little remarkable, that the point of the entrance of the Optic nerve should be deficient in the power of receiving distinct visual impressions; whilst the "yellow spot," the position of which according to Landolt is 3·905 mm. to the outer side of the optic disc, and 0·785 mm. higher, is the most sensitive portion of the entire Retina.‡

574. *Eidoptometry.*—The *limits* of Human Vision, as regards the minuteness of the objects of which it can take cognizance, have been investigated by Professor Ehrenberg, with the view of calculating the ultimate power of the Microscope.§ In opposition to the generally received opinion, Ehrenberg arrived at the conclusion that, in regard to the extreme limits of vision, there is little difference amongst persons of ordinarily good sight, whatever may be the focal distance of their eyes. The smallest square magnitude usually visible to the naked eye, either of white particles on a black ground, or of black upon a white or light-coloured ground, is about the 1-405th of an inch. It is possible, by great condensation of light, and excitement of the attention, to recognize magnitudes between the 1-405th and 1-540th of an inch, but without sharpnesss or certainty. Bodies which are smaller than these cannot be discerned with the naked eye when single, but may be seen when

* Salzer, "Sitzungsb. d. k. Akad. d. Wiss. zu Wien.," Band lxxxi. 1880, January.

† Kuhnt, Gräfe's "Archiv f. Ophth.," 1879, gives a much lower number, estimating that at the choroidal ring the optic nerve only possesses from 31,400–40,000 fibres.

‡ Aubert and Förster (v. Gräfe's "Archiv f. Ophth.," Band vii. 1860, p. 152) have shown that the acuteness of vision in receding from the fovea centralis does not diminish in concentric circles, but more quickly above and below, and more gradually towards the out and the inside. They found also that the more remote any object was from the optic axis the larger it must be to be recognized, and further, that a small object in proximity to the eye can be recognized at a greater distance from the axis than a larger object remote from the eye. The measure of acuteness of vision in general use amongst ophthalmic surgeons is a series of letters, the thickness of which is one-fifth of their height, and which are placed at such a distance that they subtend an angle of 5′. The distance d at which such letters are still distinctly recognized divided by the distance D at which they subtend an angle of 5′ expresses the sharpness of vision. Thus, if the letters C, or G, or B, be made of such a size that at 20 feet they subtend an angle of 5′, and can be read at that distance, the vision of the experimenter is regarded as being perfect, $V = \frac{d}{D}$ or $\frac{20}{20} = 1$; but if he can only see them at 10 feet his vision $= \frac{10}{20} = \frac{1}{2}$; if only at 5 feet his $V = \frac{5}{20} = \frac{1}{4}$, and so on. The absolutely smallest visual angle at which any object can under exceptionally favourable circumstances be seen subtends an angle of 50″. (Hirschmann, 1867.)

§ Taylor's "Scientific Memoirs," vol. i. p. 576. See also Helmholtz, "Physiolog. Optik.," 1860.

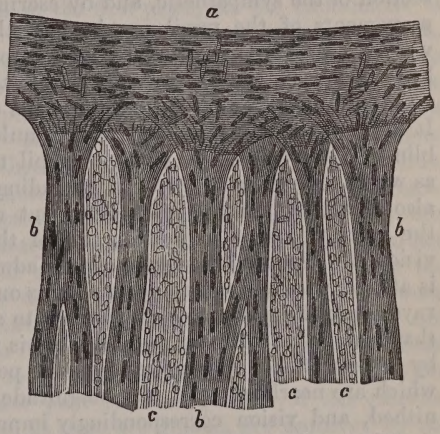
placed in a row. The degree of illumination is of essential importance, since, if sufficiently bright, extremely small points can be recognized: thus gold dust, the particles of which do not exceed 1-1125th of an inch, may be discerned with the naked eye in common daylight, whilst many of the fixed stars have no appreciable visual angle. The delicacy of vision is far greater for *lines* than for mere points; since opaque threads of 1-4900th of an inch in diameter (about half the diameter of the silkworm's fibre) may be discerned with the naked eye, when held towards the light. The size of the retinal image in these cases must be exceedingly small. In some of Bergmann's experiments it was found that black and white chequers of 1-25th of an inch square could be discerned at such a distance that the retinal image of each square could not have exceeded half the diameter of one of the cones of the bacillary layer.* A difference of illumination amounting to 1-10th for all moderate degrees of light is recognizable by the retina. Thus the addition of one candle to ten, or of ten to one hundred candles, is perceived. The degree in which the *attention* is directed to them has a great influence on the readiness with which very minute objects can be perceived; and Ehrenberg remarks that there is much greater difference amongst individuals in this respect, than there is in regard to the absolute limits of vision. Many persons can distinctly see such objects, when their situation is exactly pointed out to them, who cannot otherwise distinguish them; and the same is the case with persons of acuter perception, with respect to objects at distances greater than those at which they can see most clearly. "I myself," says Ehrenberg, "cannot see 1,2700th of an inch, black or white, at twelve inches' distance; but having found it at four or five inches' distance, I can remove it to twelve inches, and still see the object plainly." Similar phenomena are well known in regard to a balloon or faint star in a clear sky, or a ship in the horizon: we can easily see them after they have been pointed out to us; but the faculty of readily descrying objects depends on the habit of using the eyes in search of them, and of attending to the sensory impressions thus received. Aubert† found that the excitability of the retina for extremely feeble stimuli rapidly attained a high degree when a dark room was entered, though a slight increase in sensitiveness continued to take place for a considerable period if the sojourn in it were protracted. A wire heated by electricity was first discovered when at a temperature of about 666° F. In another series of experiments he found that the feeblest illumination of the field of vision that could be recognized was about equal to that of the planet Venus when brightest, or to the white light of day admitted into a chamber through an opening forty-one seconds square. Small surfaces, however, always require considerably greater illumination, in order that they should be perceived, than large.

575. The amount of light admitted to the eye is regulated by the contraction and dilatation of the Pupil, the smallest diameter of which is about 1-20th, and its largest about 1-3rd of an inch. The arteries of the Iris are derived from the long ciliaries, and in part from the short ciliaries and the veins, whilst chiefly joining the venæ vorticosæ, and thus returning the blood they contain by the ophthalmic veins, discharge their contents in part also into the canal of Schlemm, and thus returns a portion of their blood by the facial vein. These vessels constitute the substance of the iris. A layer of somewhat inbricated oval epithelial cells, with round nuclei, covers the anterior surface in the infant, but is distinguishable with difficulty, or is only partially present, in the adult. Posteriorly is a distinct layer of pigment cells. The limits of these are so ill-defined as to have led some to describe

* Henle and Meissner's "Bericht," 1857, p. 559. † "Physiologie der Netzhaut," 1864.

them as forming a uniform sheet of protoplasm with pigment granules distributed through its substance. Owing to the presence of this pigment, the iris is absolutely opaque. The Iris is well supplied with nerves derived from the 3rd, 5th and sympathetic, most of the larger trunks lying in front of the blood-vessels.* They enter the Iris from the ciliary muscle, and form five circular concentric plexuses connected by radial fibres from which delicate primitive fibrils are given off, ending in a terminal network covering the whole of the iris. Formad was unable to discover any ganglionic cells. The muscular structure of the Human *Iris* is entirely of the non-striated kind, being composed of the elongated fibre-cells with staff-shaped nuclei which are characteristic of that variety. Part of these are so disposed as to form a circular sphincter (Fig. 270, *a*), which can be readily seen in the iris of the white rabbit, or in the blue iris of man from which the uvea has been removed, immediately surrounding the pupillary margin to the breadth of about one-third of a line. The fibres of this sphincter are not absolutely parallel, especially at the outer margin, where they seem to become continuous with those of the radiating fasciculi (*b b*), which may be traced from this sphincter (though usually with difficulty) to the outer margin of the iris, sometimes anastomising with each other in their course.† The contraction of the annular fibres, whereby the diameter of the pupil is *diminished*, is effected, as already explained, through the instrumentality of the Third pair of nerves; the contraction of the radiating fibres, on the other hand, whereby the pupil is *dilated*, is under the government of the cervical portion of the Sympathetic, being called forth‡ by irritation of the trunk of the Sympathetic in the neck, or of the lower part of the cervical portion of the Spinal cord, by the magneto-electric apparatus; whilst section of the Sympathetic produces a permanent contraction of the pupil, the action of the Third pair being then no longer antagonized. It appears, from other experiments, that the fibres through which this movement is effected, pass through the Gasserian ganglion, and are distributed to the eye by the ophthalmic branch of the Fifth pair. The contraction of the Pupil is thus a reflex action, induced by excitation of the retina, and acting through the nervous circle formed by the optic nerves and tracts, and the third pair of cerebral nerves. Whilst admitting that the movements of the Iris are essentially effected by muscular tissue, it must be acknowledged that its extreme vascularity renders

Fig. 270.



Muscular structure of the Iris of a White Rabbit:—*a*, sphincter of the pupil; *b*, *b*, radiating fasciculi of dilator muscle; *c*, *c*, connective tissue with its corpuscles.

* Formad, 'Distribution of Nerves in the Iris,' "Amer. Journ. of Med. Sci.," 1878, January, p. 97. In this paper the literature of the subject is excellently given.

† See Prof. Kölliker's "Mikroskopische Anatomie," Band ii. § 272; and Jos. J. Lister's 'Observations on the Contractile Tissue of the Iris,' in "Quart. Journ. of Microscop. Science," vol. i. p. 8. See "Lancet," vol. i. 1870, pp. 127 and 211.

‡ See Budge and Waller, "Gazette Médicale," 1851, Nos. 41, 44; and Wagner, "Journ. de Physiologie," 1860; Franck, "Comptes Rendus," 1879, p. 1016.

it highly susceptible of either local or general changes in the pressure of the blood. Fabricius of Aquapendente likened the closure of the pupil to the turgescence of erectile tissue, and his opinion has been supported by such observers as Portal, Bichat, and Haller; but the activity this movement presents is too great to be thus explained; and it would seem that, whilst contraction of the pupil is mainly effected by the sphincter innervated by the Third, it may also be aided by vascular dilatation. Thus it may be caused by section of the sympathetic, or even by merely hanging the head down, by puncturing the Eye, and reducing the intra-ocular tension by allowing the escape of the aqueous, and it occurs in Iritis. On the other hand, the pupil is dilated in glaucoma, in which the intra-ocular tension is augmented; and it has been observed by Bernard* that contraction of the pupil can be easily induced after section of the Third nerve by paracentesis of the cornea, section of the sympathetic, and by eserine. It would hence appear that the movements of the pupil are in part the result of variations in the size of vessels which are governed by the sympathetic, and which there is reason to believe may be excited through the Fifth. The two pupils contract consentaneously, light falling on either retina causing the opposite Eye to contract. It is remarkable, also, that the stimulus of light applied to a perfectly blind Eye will cause the opposite pupil to contract. It answers the purpose, as we have seen, not merely of excluding superfluous light from the eye, but also of cutting off the most divergent rays when the object is brought near the refracting surface (§ 567), and of thus preventing the indistinctness of vision which would result from their admission. For although, when the Eye is at rest, parallel rays come to a focus on the Retina, divergent or convergent rays proceeding from any point come to a focus either behind or in front of that membrane, forming upon it what is termed a "circle of diffusion;" but by cutting off the outermost rays and permitting the entrance of those only which are nearly parallel, the magnitude of such circles is materially diminished, and vision correspondingly improved. It is interesting to observe that contraction of the pupil is effected with greater rapidity than dilatation, a matter of some importance in sudden alternations from light to darkness. The iris contracts and the pupil becomes smaller when light falls on the retina; when accommodation is made for near objects; when the eyes are made to converge; during sleep, under the action of certain medicinal agents, as eserine, nicotin, opium, and pilocarpin;† and in hyperæmic conditions of its vessels, the iris dilates, the pupil becoming larger in the absence of light; on powerful stimulation of sensory nerves during violent muscular effort in dyspnœa; in conditions leading to anæmia of the vessels of the Iris, in certain mental emotions, as fear; and as the result of the action of atropine, duboisia, and other drugs. M. Brown-Séquard‡ has shown that the Irides of various animals may be directly affected by Heat and Light. Thus, if the eyes of dogs, cats, or rabbits, either soon after death, or shortly after their removal from the body, be suddenly exposed to an alteration of temperature amounting to 50° or 60° F., if the pupil be contracted, it expands; though, on the contrary, if it be in the first instance dilated, it speedily contracts. These effects of heat have not been observed either in Man or the Mammalia during life. As regards the direct action of Light, Brown-Séquard found that the Irides of eels and frogs which had been removed for several (even sixteen) days from the body

* See also for a consideration of this subject a pamphlet by Debouzy entitled "Considérations sur les Mouvements de l'Iris," 1875; and one by Piercepied, "De la Mydriasis," 1876.

† Galizowski, "Gaz. des. Hopit.," 1877, Nov. 6.

‡ "Journal de la Physiologie," 1859, vol. ii. p. 294.

in winter, as well as the Irides of mammals and birds for a short time after death, contracted on exposure to the light of the sun or of a candle; this effect being produced even when the posterior half of the eye had been cut off, and when, therefore, there could have been no reflex action. The yellow rays appeared to have the greatest energy. These remarkable phenomena prove, at all events, that the contraction of the pupil is not, as has occasionally been maintained, exclusively due to vascular turgescence. The cause of the effect produced by Light is difficult to explain, but that occasioned by Heat may perhaps be attributed, as Brown-Séquard suggests, to the circumstance that a contracted muscle has less power than one in a state of extension, so that if a stimulus act equally on both, when previously nicely balanced in point of strength, the uncontracted muscle will exert the greater force, and consequently overpower the contracted muscle.

576. The sense of Vision depends, in the first place, on the excitement of our sensational consciousness by the ocular picture impressed upon the retina, which represents the outlines, lights and shades, colours, and relative positions of the objects before us; and all the ideas respecting the real forms, distances, &c., of bodies, which we found upon these data, are derived through the perceptions, either instinctively or experientially suggested by sensations. Many of these ideas are derived through the combination, in our minds, of the Visual perceptions, with those derived from the sense of Touch. Thus, to take a most simple illustration, the idea of *smoothness* is one essentially tactile; and yet it constantly occurs to us, on looking on a surface which reflects light in a particular manner. But if it were not for the association, which experience leads us to form, of the connection between *polish* as seen by the *eye*, and *smoothness* as felt by the *touch*, we should not be able to determine, as we now can do, the existence of both these qualities from an impression communicated to us through either sense singly.—The general fact that, in Man, the greater part of those notions of the external world, by which his actions in the adult state are guided, are acquired by the gradual association of the two sets of perceptions derived through the Sight and through the Touch, is substantiated by amply sufficient evidence; this being chiefly derived from observations made upon persons born blind, to whom sight has been communicated by an operation, at a period of life which enabled them to give an accurate description of their sensations. The case recorded by Cheselden is one of the most interesting of these. The youth (about twelve years of age), for some time after tolerably-distinct vision had been obtained, saw everything *flat* as in a picture, simply receiving the consciousness of the impression made upon his retina; and it was some time before he acquired the power of judging, by his sight, of the real forms and distances of the objects around him. An amusing anecdote recorded of him shows the complete want which there is in Man, of any natural or intuitive connection between the ideas formed through visual and through tactile sensations. He was well acquainted with a Dog and a Cat by *feeling*, but could not remember their respective characters when he *saw* them; and one day, when thus puzzled, he took up the Cat in his arms, and felt her attentively, so as to associate the two sets of ideas, and then setting her down, said, 'So, puss, I shall know you another time.'—A similar instance has come under the Author's own knowledge; but the subject of it was scarcely old enough to present phenomena so striking. One curious circumstance was remarked of him which fully confirms (if confirmation were wanting) the view here given. For some time after his sight was tolerably clear, the lad preferred finding his way through his father's house (to which he had been quite accustomed when blind)

by touch rather than by sight, the use of the latter sense appearing to perplex instead of assisting him; but, when learning a new locality, he employed his sight, and evidently perceived the increase of facility which he derived from it.*—The actions performed by many new-born animals do not constitute any valid objection to the view that such visual perceptions are for the most part *acquired* by Man; for all that is indicated by them is, that certain sensations give rise to movements adapted to supply the wants to which they relate; and they do not afford any proof that definite notions, such as we entertain, of the forms and properties of external objects are possessed by the animals which exhibit them.—We shall now examine, a little more in detail, into the means by which we gain such notions, and the data on which they are founded.

577. The first point to be determined is one which has been a fruitful source of discussion—the cause of *erect vision*, the picture upon the retina being inverted; and with this is connected the general question of the origin of our *Sense of Direction*.—The difficulty which has been raised in regard to the former subject is rather apparent than real; being founded on an erroneous notion of the nature of the Visual sense. For it seems to have been supposed that we *look at* the retinal picture with the 'mind's eye,' just as we look at the picture formed by a Camera with the bodily eye; and that our consciousness must be therefore impressed by its discordance with the information which we receive through our sense of Touch. Some philosophers, indeed, have actually gone so far as to assert that the Infant must at first see everything inverted, and that the erectness of visual objects is only learned by the corrective experience gained by touching and handling them. But such is clearly not the case; for the visual perception is obviously not a mere *transfer* of the sensorial impression, but is a *mental state excited by it*, and therefore related to it as an effect to its cause; and we know no reason why it should be *less natural* for the retinal picture to *suggest to the mind* the notion of *erect* position, than for it to have the contrary effect. Moreover, it will appear from investigations to be hereafter detailed (§ 594), that there is in the eye a 'common centre of direction,' through which all lines must pass, that are drawn from any points of an external object to the corresponding points of its retinal image;† and that we immediately refer the cause of the excitation of any spot of the retina by a luminous impression, to an objective source in the 'line of direction' which passes from that spot through the centre of direction; so that, in virtue of this 'law of visible direction,' as all the lines of direction cross each other both vertically and laterally, the formation of an inverted image upon our retina suggests to our minds the representation of the object in its erect position, and the same reversal takes place also in regard to its two sides, which are transposed in the retinal picture. A peculiar

* The question has been proposed, whether a person born blind, who was able by the sense of Touch to distinguish a cube from a sphere, would, on suddenly obtaining his Sight, be able to distinguish them by the latter sense. This question was answered by Locke in the negative; and, as appears from the facts above stated, with justice.

† With regard to the precise situation of this 'centre of direction,' there is a want of accordance among those who have attempted to determine it; some having placed it in the centre of the pupil, others in the centre of the crystalline lens, others at various distances between this and the centre of the globe, and others (among them Sir D. Brewster) *in* the centre of the globe. This last notion, with the 'law of visible direction' founded upon it—which affirms that every object is seen in the direction of the perpendicular (or radius) to every point of the retina which is impressed—is so manifestly wrong, that it is difficult to conceive how it could ever have been entertained by men of science. The experimental investigations of Listing indicate a point near the centre of the crystalline as the 'centre of direction' (§ 563).

arrangement of the receptive apparatus, which seems to be subservient to this mental appreciation of direction, has been already noticed.

578. The cause of *Single Vision with the Two Eyes* has, in like manner, been the subject of much discussion; and here, too, the difficulty is rather apparent than real, having for its foundation the idea that the mind looks at the two retinal pictures as at two separate objects, instead of being impressed by a certain state of the Sensorium, which may be excited through the instrumentality of either eye, or through that of both in combination. Some have even asserted, under the influence of this idea, that we do not really employ both eyes simultaneously, but that the mind is affected by the image communicated by one only; which might seem to be confirmed by the fact sufficiently well ascertained respecting the alternate use of the two eyes, when they are looking through two differently-coloured media. But of this assertion a complete disproof is afforded by the knowledge we now possess (§ 580), that our appreciation of the solid forms of bodies depends on the combination, *by the Mind*, of the images simultaneously suggested by the two pictures; and that our knowledge of distances is in great part obtained by like manner.—Attempts have been made to explain the phenomena of Single Vision by the peculiar decussation of the Optic Nerves formerly described; it being supposed that only one Optic Ganglion would be affected by an impression made upon both Retinæ.* This explanation, however, even supposing the fact to be as stated, would be far from affording the solution of the problem; and it would be entirely inapplicable to that very important series of phenomena to be next described, which show how large an amount of information we derive, not from the *repetition*, but from the *difference*, of the sensory impressions made by the same object upon our two retinæ; and which indicate that here, as in the case of erect vision, the *mental interpretation* of the sensory impressions is a process altogether removed from the simple affection of the consciousness by those impressions, and is not to be accounted for by any structural arrangements of the Sensorial apparatus. One condition of single Vision, however, seems to be this, that the two images of the object should be formed on parts of the two retinæ which are *accustomed* to act in concert; and *habit* appears to be the chief means by which this conformity is produced. There can be no doubt, however, that double images are continually being conveyed to the Sensorium; but that, from their want of force and distinctness, and from the attention being fixed on something else, we do not take cognizance of them. This may be shown by a very simple experiment. If two fingers be held up before the eyes, one in front of the other, and vision be directed to the more distant, so that it is seen singly, the nearer will appear double; while, if the nearer one be regarded more particularly, so as to appear single, the more distant will be seen double. A little consideration will show, therefore, that our minds must be thus continually affected with sensations, which cannot be united into the idea of a single image; since, whenever we

* This decussation seems to be, in some cases, more complete than in others, for in various experiments made by Dr. Waller upon the effects of section of one optic nerve, it was found that the *Optic Tract* upon the same side as the lesion, showed no signs of degeneration, whilst that of the opposite side soon underwent disorganization with the exception of a few strands on the inner and posterior aspect; thus countenancing the opinion that there are commissural fibres passing between the corpora quadrigemina of the two sides, but negativing the view that some of the fibres from each retina run to the corpora quadrigemina on their own side. Dr. Waller is inclined to think, therefore, that the decussation is complete. It is important to observe, that in these experiments the anterior portion of the divided nerve, with the retinal elements, remained unchanged for many weeks. See "Proceedings of the Royal Society," vol. viii. On the other hand, the reader may refer to some curious cases of partial Amaurosis recorded by Mr. Towne in the "Guy's Hospital Reports" for 1863, p. 127.

direct the axes of our eyes towards any object, almost everything else will be represented to us as double; but we do not ordinarily perceive this, from our minds being fixed upon a clear and distinct image, and disregarding, therefore, the vague undefined images formed by objects not in the visual focus. Of this it is very easy to satisfy one's-self. The above experiment, moreover, makes it evident that double vision cannot result from *want of symmetry* in the position of the images upon the retina, to which some have attributed it; for it answers equally well, if the line of the two fingers be precisely in front of the nose, so that the inclination of both eyes towards either object is equal; the position of the images of the second object must then be at the same distance on either side from the central line of the retina, and yet they are represented to the mind as double. Hence, too, it seems clear that singleness of vision in an object that is *looked-at*, is also dependent in part upon the *convergence of the optic axes* in that object (§ 568); and that this is the case appears further from a curious experiment devised by Prof. Wheatstone, in which two similar objects are made to seem as one, when they are placed in the line of convergence. This is accomplished by looking through two tubes, placed before the right and left eyes respectively, at two similar objects of any description, placed near the farther extremities of the tubes; if, now, these objects be slightly approximated, so that the axes of the tubes (still directed towards them) meet in a point beyond, the mind is impressed with the image of only a single object, and this appears to be removed back to the point of convergence. It has been found by Gehler, J. Müller, and others, that those objects which do not appear double when a given point is fixedly regarded, are situated in a certain circular line, termed the Horopter, of which the chord is formed by the distance between the eyes, whilst the magnitude of the circle is determined by three points—namely, by the two eyes and the point towards which their axes converge. Prof. Helmholtz, however, considers that generally the Horopter is a line of double curvature, produced by the intersection of two hyperboloids, or exceptionally, of two plane curves; and that when we look straight forward to a point of the horizon, the Horopter becomes a horizontal plane passing through our feet—being, in fact, the ground on which we are standing. The form and situation of the Horopter appear to be of great practical importance in enabling us to judge with accuracy of the shape and distance of those objects which are situate in it.*

579. On the mode in which our notion of the *solid forms* and *relative projection* of objects is acquired, great light has been thrown by the interesting experiments of Prof. Wheatstone.† It seems perfectly evident, both from reason and experience, that the flat picture upon the retina, which is the immediate source of our sensation, could not itself convey to our minds any

* See Müller's "Physiology," translated by Dr. Baly, vol. ii. p. 1196; also the Croonian Lecture for 1864, delivered before the Royal Society, by Professor Helmholtz, in vol. xiii. of the "Proceedings of the Royal Society," and Dr. H. Kaiser in "Archiv f. Ophth.," Band xv. 1869, p. 75. Dr. Kaiser, who has treated the subject analytically, states that the interior system of the Horopter is an hyperbole of equal dimensions for each eye; one of the radii of which passes through the fovea centralis and never passes through the punctum cæcum; its summit is found at the side of the fovea. The real axes have the same angle between them as that of the two retinal horizons, their inclination on this does not differ much from half a right angle. In individual cases it is found that for a point of fixation situated at an infinite distance, the Horopter becomes a spherical surface with an infinite radius. Thus in looking at a star all the stars are found on the Horopter. For a point of fixation situated in the primary position of the retinal plane, the Horopter becomes reduced to a circle, the circle of the Horopter of Müller passing through the centre of each globe and the fixed point. For a point of fixation situated in the median plane, the Horopter is an ellipse situated in a plane which bisects the angle formed by the visual plane and the primary position.

† "Philosophical Transactions," 1838 and 1852.

notion but that of a corresponding plane surface. In fact, any notion of *solidity*, which might be formed by a person who had never had the use of more than one eye, would entirely depend upon the combination of his visual and tactile sensations. This view is fully confirmed by the case already referred to (§ 576), as recorded by Cheselden. The first visual idea entertained by the youth was, that the objects around him formed a flat surface, which touched his eyes, as they had previously been in contact with his hands; and after this notion had been corrected, through the education of his sight by his touch, he fell into the converse error of supposing that a picture, which was shown to him, was the object itself represented in relief on a small scale.—But where both eyes are employed, it has been ascertained by Prof. Wheatstone, that they concur in exciting the perception of solidity or projection, which arises from the *mental* combination of the two *dissimilar* pictures formed upon the two retinæ. It is easily shown, that any *near* object is seen in two different modes by the two eyes. Thus let the reader hold up a thin book, in such a manner that its back shall be exactly in front of his nose, and at a moderate distance from it; he will observe, by closing first one eye and then the other, that his perspective view of it (or the manner in which he would represent it on a plane surface) is very different, according to the eye with which he sees it. With the right eye he will see its right side, very much fore-shortened; with the left he will gain a corresponding view of the left side; and the apparent angles, and the lengths of the different lines, will be found to be very different in the two views. On looking at either of these views singly, no other notion of solidity can be acquired from it, than that to which the mind is conducted, by the association of such a view with the touch of the object which it represents. But it is capable of proof, that the mental association of the *different* pictures upon the two retinæ, does of itself give rise to the idea of solidity. This proof is afforded by Prof. Wheatstone's ingenious instrument, the Stereoscope, first described by him in 1838.*

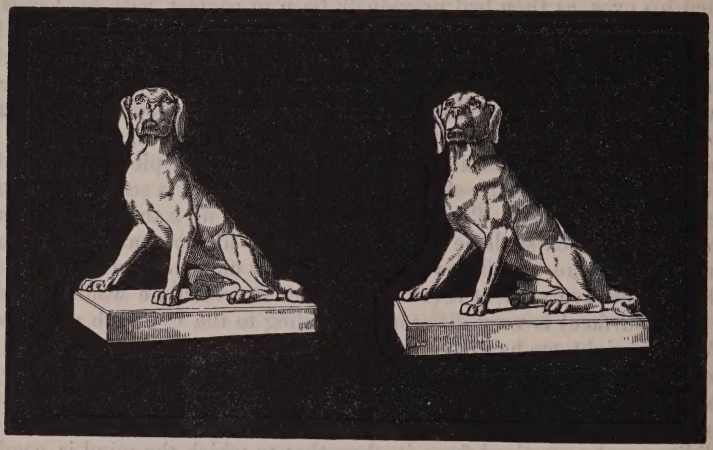
580. The *Stereoscope* in its original form essentially consists of two plane mirrors, inclined with their backs to one another, at an angle of 90°. If two perspective drawings of any solid object, as seen at a given distance with the two eyes respectively, such as those at A and B, Fig. 271, be so placed before these mirrors, one before each, that their two images shall be made to fall upon the corresponding parts of the two retinæ, in the same manner as the two images formed by the solid object itself would have done, the mind will perceive, not a single representation of the object, nor a confused blending of the two, but a projecting or receding surface, the exact counterpart of that from which the drawings were made.† The solid form if forcibly impressed on the mind, even when outlines only are given, especially if these be

* Various modifications of this instrument have been subsequently introduced; and there is one which has come into very extensive use, in which the two monocular pictures placed side by side, as in Figs. 271, 272, are viewed by the two eyes respectively through two halves of a convex lens. The great advantage of this instrument is its portability, and its enlargement of the pictures by the magnifying power of the lenses; but it is limited to pictures of small size, since the distance between corresponding points of the two pictures must not exceed the distance between the centres of the two eyes; and it is incapable of many adaptations which can be made with the mirror-stereoscope. In the Stereomonoscope of Claudet, the idea of relief is obtained by looking with both eyes at once on a ground-glass plate at the image produced by the coalescence of the two images of a stereoscopic slide, each refracted by a separate lens.—See "Proceed. of Royal Society," vol. ix. 1857–59, p. 194.

† The most striking effect is produced by two photographic pictures, taken at the same time by two cameras, so placed that their axes shall form the same angle with each other as that which the axes of the two eyes would form when looking at the same object. This adaptation, though the credit has been assumed by others, was originally devised by Prof. Wheatstone.

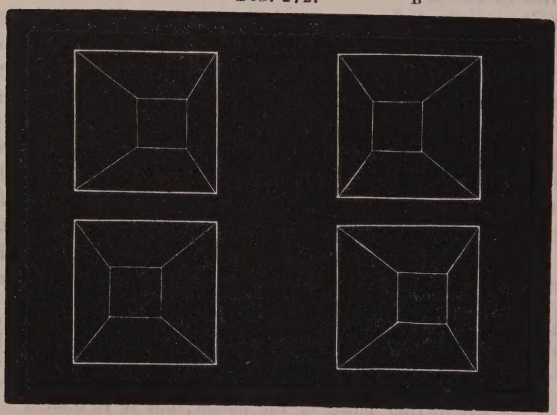
delineations of simple geometrical figures, easily suggested to the mind; and it may be readily shown that the very same outlines will suggest different conceptions, according to the mode in which they are placed. Thus in Fig. 272, the upper part of figures A, B, when combined in the Stereoscope, excite the idea of a *projecting* truncated pyramid, with the small square *in the centre*,

A FIG. 271. B



and the four sides sloping equally *away from* it; whilst the lower pair of figures, C, D, which are the same as the upper, but transferred to the opposite sides, no less vividly bring before the mind the visual conception of a *receding* pyramid, still with the small square in the centre, and the four sides sloping equally *towards* it. — Prof. Wheatstone has further shown, by means of the Stereoscope, that similar images, differing to a certain extent in magnitude, when presented to the corresponding parts of the two retinæ, give rise to the perception of a single object, intermediate in size between the two monocular pictures. Were it not for this, objects would appear single only when at an equal distance from both eyes, so that their pictures upon the retinæ are of the same size; which will not happen unless they are directly in front of the median line of the face. Again, if pictures of dissimilar objects be simultaneously presented to the two eyes, the consequence will be similar to that which is experienced when the rays come to the eye through two differently coloured media; the two images do not coalesce, nor do they appear permanently superposed one upon the other; but at one time one image predominates to the exclusion of the other, and then the other is

A FIG. 272. B



C D

seen alone ; and it is only at the moment of change that the two seem to be intermingled. It does not appear to be in the power of the Will, Prof. Wheatstone remarks, to determine the appearance of either ; but if one picture be more illuminated than the other, it will be seen during a larger portion of the time. If, however, the differences in the two pictures be such that the Mind can reconcile them, an *intermediate* conception is formed ; thus if two photographic portraits be taken at the proper angle for the Stereoscope, not simultaneously but consecutively, and the "sitter" alter his expression in the interval, so that one of the portraits represents him with a smile, and the other with a frown, the Stereoscopic image will present an intermediate expression of placidity*.—Many other curious experiments with this simple instrument are related by Prof. Wheatstone ; and they will go to confirm the general conclusion, that the combination of the dissimilar images furnished by the two eyes is *a mental act*, the resultant of which, in the case of all objects that are near enough to be seen in different perspective with the two eyes, is a mental image (referred to the visual sense) possessing the attributes of solidity and projection. In regard to distant objects, however, the difference in the images formed by the two eyes is so slight that it cannot aid in the determination ; and hence it is, that whilst we have no difficulty in distinguishing a picture, however well painted, from a solid object, when placed near our eyes (since the idea which might be suggested by the image formed on one eye will then be corrected by the other),† we are very liable to be misled by a delineation in which the perspective, light and shade, &c., are faithfully depicted, if we are placed at a distance from it, and are prevented from perceiving that it is *but* a picture.‡ In this case, however, a slight movement of the head is sufficient to undeceive us ; since by this movement a great change would be occasioned in the perspective view of the object, supposing it to possess an uneven surface ; whilst it scarcely affects the image formed by a picture. In the same manner, a person who only possesses one eye, may obtain, by a slight motion of his head, the same idea of the form of a body which another would acquire by the simultaneous use of his two eyes.§

581. Our appreciation of the relative Distances of *near* objects seems to be derived in like manner from the mental combination of the perceptions derived from the dissimilar pictures upon the two retinæ, assisted by the sensations derived from the muscles of the eyeballs, which are put in action to bring the optic axes into the requisite convergence. How much our right estimation of the relative distances of objects not too far from the eye depends upon the joint use of *both eyes*, is made evident by the fact that, if we close one eye, we find ourselves unable to execute with certainty many actions (such as threading a needle, or snuffing a candle) which require its guidance. In proportion as the object is approximated to the eyes, slight differences of distance produce marked differences in the degree of convergence, and these are readily appreciated so as to afford the means of very nice discrimination ;

* See Galton, 'Composite Portraits,' "Nature," vol. xviii. 1878, p. 97.

† It is a remarkable illustration of this principle, that a photographic representation of a landscape, building, &c., when viewed with *one eye* at a moderate distance, frequently brings the real scene far more forcibly before the mental vision than when it is looked at with both eyes ; since, in the latter case, the mind cannot avoid perceiving the flatness of its surface ; whilst in the former, the perspective, and the distribution of the lights and shadows, are free to suggest to the mind the relative distances and projections of the several parts.

‡ This delusion has been extremely complete, in some of those who have seen the panoramic view of London in the Colosseum. A lively and interesting account of it is given in the Journal of the Parsee Shipbuilders, who visited England some years ago.

§ For many interesting experiments with the stereoscope, see Mr. T. Towne in "Guy's Hospital Reports" for 1862 and 1863.

whilst, on the other hand, in proportion as they are removed farther and farther, do the optic axes approach parallelism, and the power of appreciating differences of distance is lost. It is the usual opinion that the muscular sensation which accompanies the inclination of the optic axes, *immediately suggests* the notion of the *distance* of an object; and that our appreciation of its *size* depends upon a secondary *interpretation* of the magnitude of its picture on the retina, on the basis of this notion. But it would appear from the experiments of Professor Wheatstone, that the reverse is the case; the sensation of convergence assisting in the first instance to determine the size, and the appreciation of distance being a secondary judgment based on this foundation (§ 584).—The power of estimating distance from the foregoing data, however, is obviously, in Man, not an intuitive but an acquired endowment; for it is evident to any observer, that infants, or older persons who have recently acquired sight, form very imperfect ideas respecting the distance of objects; their attempts to grasp bodies which attract their attention being for a long time unsuccessful, so that they only gradually learn to measure distances by the sight, through the medium of the touch. And it seems to follow from this, that even the notion of 'projection,' which we seem necessarily to form when looking at a solid object within a moderate distance, or at a properly-adjusted pair of Stereoscopic pictures, is not derived from an original intuition, but is the result of the association of our visual with our tactile experience, very early in life, so as to constitute a 'secondary intuition' on which all our subsequent appreciation of projection is based.

582. In regard to *remote* objects, our judgment of Distance is chiefly founded upon their apparent size, if their actual size be known to us; but, if this be not the case, and if we are so situated that we cannot judge of the intervening space, we principally form our estimate from that effect of different degrees of remoteness upon the distinctness of their colour and outline, which is known to Artists as 'aerial perspective.' Hence this estimate is liable to be greatly affected by varying states of the atmosphere, as is particularly known to every one who has visited warmer climates; where the extreme clearness of the air sometimes brings into apparently-near proximity a hill that rises some miles beyond a neighbouring ridge (the intervening space being hidden, so as not to afford any datum for the estimate of the distance of the remote hill), whilst a slight haziness carries its apparent distance to three or four times the reality. Additional means of judging of the distance of remote objects pointed out by Aubert,* are found in their parallax or apparent change of place, on the alteration of our own position with regard to them, and in the rate of movement, both absolute and relative, of the objects themselves, if they happen to be in motion.

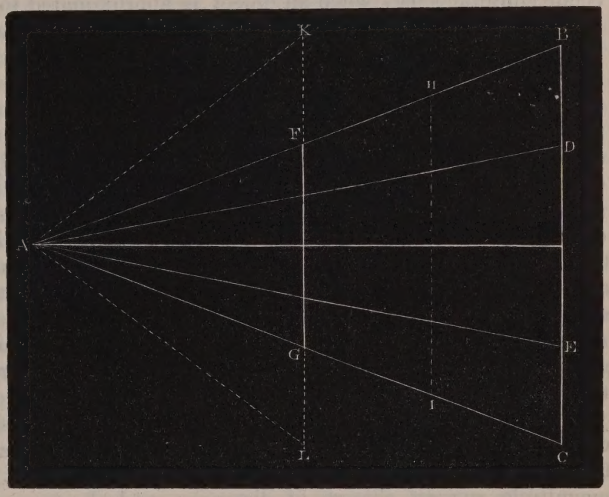
583. Our estimate of the Size of a *remote* object is partly dependent upon the *visual angle* under which we see it, and partly upon our estimate of its *distance*.† The 'visual angle,' formed by imaginary lines drawn from the eye (Fig. 273, A) to the extreme points, B, C, of the object, is the measure of the dimension of its image upon the retina; and it is obvious that, if two

* "Physiologie der Netzhaut," 1864, p. 17.

† When objects are so remote that we have no means of even approximately estimating their *distance*, we have no measure whatever of their *size*. Thus, the Sun and the Moon are of nearly the same apparent size to us, though one is about four hundred times the distance of the other; and we may cover either disc with a sixpence held near the eye, so as to be seen under the same visual angle; but we do not possess the least power of estimating the actual sizes of these objects, save by a calculation based on a knowledge of their relative distances.

objects, B C, D E, the former twice the length of the latter, be placed at the same distance, the visual angle B A C being twice as great as the angle D A E, the image of B C upon the retina will be twice as long as that of D E, and the mind will estimate their relative sizes accordingly. But if the distance of the object D E from the eye be diminished to one-half, so that it is brought into the position F G, its visual angle, and consequently the size of its image on the retina, will now be equal to that of B C; and the estimate we form of the relative sizes of the two will entirely depend upon the idea we entertain of their relative distances. Hence any circumstance which modifies that idea, produces a corresponding difference in our estimate of their size; so that the apparent size of an object, seen under a given visual angle, may be estimated as larger or smaller than the reality, according as we suppose it to be more or less distant than it really is. Of this we have a familiar instance in the fact, that if we meet a child whilst we are walking across a common in a fog (the flatness of the ground not giving us much power of estimating the intervening space), it appears to have the stature of a man, and a man seems like a giant; for the indistinctness of outline causes the mind to conceive of the figures as at a greater distance than they really are, and their apparent dimensions are augmented in like proportion. For if the object F G (Fig. 273) be *mentally carried-back* to the distance of D E, being still seen under the visual angle F A G (or B A C), it will appear to possess the length B C instead of D E. On the other hand, if the object B C were to be *mentally brought-forward* into the position K L, its apparent size being still determined by its visual angle, it will seem to be reduced to the length F G. That our estimate of the Size of *near* objects, however, depends upon a more direct process, seems to be a necessary inference from the following very ingenious experiments, made by Professor Wheatstone with a modification of his Mirror-Stereoscope, devised for separately testing the influence of the two conditions—namely, the magnitude of the retinal picture and the degree of convergence of the optic axes—which are ordinarily in action together. When an object is moved nearer to or farther from the eye, its *perceived* or estimated magnitude undergoes no change. But if two pictures, placed in the mirror-stereoscope, be made to move to and from the mirrors, in such a manner as to vary their *distances* from these (and therefore from the eyes), without altering the angle of convergence, their perceived magnitudes are augmented and reduced, in precise proportion to the increased and diminished sizes of the retinal pictures. Conversely, if the two pictures be made so to change their places in regard to

Fig. 273.



the mirrors (by moving in a horizontal circle, of which the middle-point between the mirrors is the centre), that the *angle of convergence* is increased or diminished, as it would be if the object were brought nearer to the eyes or removed farther from them, the perceived magnitude of the pictures is altered in an inverse manner; being reduced when the angle of convergence is increased, and increased when the inclination of the optic axes is lessened so as to approach parallelism. Thus it appears that the absence of alteration in the perceived magnitude of an object as ordinarily seen at varying distances, is the result of the inverse action of these two kinds of suggestion; for the enlargement of the retinal picture when acting alone, occasions an increase in the perceived magnitude, whilst an increase of convergence, taking place by itself, diminishes the perceived magnitude; and thus as these alterations occur simultaneously when an object is approximated to the eye, its dimensions seem to undergo no change; as will also be the case when, by the removal of the object to a greater distance, these conditions are again made to vary simultaneously, though in a contrary direction.—It may further be remarked, that, in the first of the foregoing experiments, the picture whose perceived magnitude is undergoing enlargement or diminution in consequence of the alteration of its retinal magnitude, seems evidently to be approaching or receding; yet if we fix our attention on it when it is stationary, at any instant, it appears to be at the same distance at one time as at another—the effect being very much like that of the Phantasmagoria, in which the alteration in the size of the images on the screen suggests the notion of their approach or recession, although we are quite sensible that the distance of the screen from our eyes remains constantly the same. In the second experiment, on the other hand, the picture whose perceived magnitude is undergoing diminution or enlargement in consequence of increase or lessening of the angle of convergence, does not appear either to approach or recede, and yet, when attentively regarded in different fixed positions, it is felt to be at different distances. Hence, as Professor Wheatstone observes, convergence of the optic axes suggests fixed distance to the mind, whilst variations of retinal magnitude suggest change of distance; and, however paradoxical it may seem, "we may perceive an object approach or recede, without appearing to change its distance, and an object to be at a different distance without appearing to approach or recede."*—A like alteration in apparent size is produced when two pairs of figures (such as those given in Fig. 272), the effect of one of which is to suggest a *projecting*, and that of the other a *receding* form, are viewed at the same time in the ordinary Stereoscope. For it will be observed that the relative size of the parts which appear to project is reduced, whilst that of the apparently-receding parts is augmented; as is particularly the case with the square truncated end of the pyramid, which is estimated by most persons as from one-third to one-half larger in each of its dimensions in the receding, than it is in the projecting pyramid, notwithstanding that the actual sizes of the squares in the two sets of figures are precisely the same. For supposing H I (Fig. 273) to represent the real side of one of the small squares, which becomes the truncated end of the pyramid; when this is brought-forward by the mind into the position K L, as the truncated top of a projecting pyramid, being seen under the visual angle H A I, its apparent size is reduced to F G; whilst, on the other hand, the very same square,

* See "Philos. Transact.," 1852, pp. 2–5. The Author thinks it well to add, that he has himself verified the above very curious results; which are scarcely less valuable contributions to the Physiology of Binocular vision, than those earlier attained by the same eminent experimentalist.

carried-back by the mind to the distance D E, as when it forms the truncated end of the receding pyramid, is mentally enlarged to the dimensions B C, the visual angle B A C being the same as H A I.

584. The large share which the Mind has in the interpretation of even such visual impressions as seem to us *necessarily* to induce particular perceptions, is further shown by a very remarkable class of phenomena, termed by Professor Wheatstone (their discoverer) *Conversions of Relief.* The simplest example of this class is presented by the alteration in the visual product of the same Stereoscopic pictures, when their positions are transposed. Thus the very same diagrams, which as placed in the upper part of Fig. 272, bring before the mind's eye the conception of a projecting pyramid, when changed to the position which they occupy in the lower part of that figure, call up the image of a receding pyramid. And a corresponding effect is produced by the reversal of any other pair of Stereoscopic pictures; all that should project being made to recede, all that should recede being made to project, *provided the converse has any meaning* which the Mind can readily appreciate.—But the same effects may be produced if the objects themselves are looked at by an instrument devised by Professor Wheatstone, and termed by him the *Pseudoscope;* the optical effect of which is, to reverse the ordinary visual relations between the near and distant parts of an object; the two conditions described in the preceding paragraph being combined inversely, so that as an object or part of an object is nearer the eye, its larger picture on the retina is accompanied by a diminished convergence of the optic axes. When the impression of a seal is looked at with this instrument, it is converted into the representation of the seal itself; or, if the seal be looked at, it presents the figure raised in relief, as in its ordinary impression. So, the inside of a cup or basin appears as a solid convex body; whilst the outside appears depressed and concave. A bust regarded in front becomes a deep hollow mask; whilst the interior of the cast of a face presents the appearance of the face in its ordinary relief. A china vase, ornamented with coloured flowers in relief, seems like a vertical section of the interior of such a vase, with hollow impressions of the flowers. The base of a brain seems concave, like the interior of the base of the skull which is its reflex; and the latter seems convex and projecting, like the base of the brain.—These and similar appearances are not always immediately perceived; and some present themselves much more readily than others. Those converse forms which we are *accustomed* actually to see, or which have a *meaning* that the mind can easily apprehend, are those which are most readily perceived. Thus, the illusion which may be produced with a bust or with the cast of a face, is not obtainable even by a lengthened pseudoscopic contemplation of the *real* face, which we cannot conceive of as thus 'turned inside out.' Another very interesting fact is, that those to whom the illusion does not at first present itself, usually find it *suddenly* come upon them after a little time, especially if they should have directed their minds to the imaginary conception of the object under its changed aspect. And, further, when the conversion has taken place, the natural aspect of the object continues to intrude itself, sometimes suddenly, sometimes gradually, and for a longer or shorter interval, when the converse will again succeed it. This is due to the involuntary alternation of the attention, between the conception suggested to the mind by the visual impressions derived from both eyes, and that which is derived from either eye singly; the latter, moreover, harmonizing with and being strengthened by our recollection of the object as we have seen it before, or (if it be new to us) by our notion of its natural appearance. A remarkable illusion in respect to the direction of lines is

exhibited in the accompanying diagram, constructed by Zöllner,* which, if regarded vertically, and still more if at an angle of 48° from the perpendicular with one eye, presents the following peculiarities:—Firstly, the dark longitudinal lines do not appear to be parallel, but to converge above and below alternately; secondly, the two halves of each oblique stria, traversing a longitudinal line, do not appear to be, as they really are, continuous with one another, but the lower half seems to be displaced downwards; and thirdly, sometimes, though not always, a stereoscopic effect is perceived, as though the lines were drawn on a sheet of paper folded longitudinally. Hering† explains this by a train of reasoning too long to be here inserted, but to the effect that all acute angles under 60°, on account of the natural curvature of the retina, appear less than they really are.

Fig. 274.

585. The *persistence* during a certain interval *of impressions made upon the retina*, gives rise to a number of curious visual phenomena, which can be here only briefly adverted to. The prolongation of the impression will be governed, in part, by its previous duration; thus, when we rapidly move an ignited point through a circle, the impression itself is momentary, and remains but for a short period; whilst, if we have been for some time looking at a window, and then close our eyes, the impression of the dark bars traversing the illuminated space is preserved for several seconds. One of the results of this persistence is the combination into a single image, of two or more objects presented to the eye in successive movements; but these must be of a kind which can be united, otherwise a confused picture is produced. Thus in a little toy, called the Thaumatrope, which was introduced some years ago, the two objects were painted on the opposite sides of a card—a bird, for instance, on one, and a cage on the other; and when the card was made (by twisting a pair of strings) to revolve about one of its diameters, in such a manner as to be alternately presenting the two sides to the eye at minute intervals, the two pictures were blended, the bird being seen in the cage. A far more curious illusion, however, was that first brought into notice by Professor Faraday; who showed that, if two toothed wheels, placed one behind the other, be made to revolve with equal velocity, a stationary spectrum will be seen; whilst if one be made to revolve more rapidly than the other, or the number of teeth be different, the spectrum also will revolve. The same takes place when a single wheel is made to revolve before a mirror, the wheel and its image answering the purpose of the two wheels in the former case. On this principle, a number of very ingenious toys have been constructed; in some of these, the same figure or object is seen in a variety of positions; and

* Poggendorff's "Annalen der Phys.," Band cx. p. 500.

† Funke's "Lehrbuch der Physiologie," vol. ii. 1866, p. 416.

the successive impressions, passing rapidly before the eye, give rise by their combination to the idea that the object is itself moving through these positions.*—It is interesting to remark, moreover, that when the eye has been for some time contemplating an object in motion, and is then directed towards stationary objects, *these* appear for a short time to have a like movement. Any railroad traveller may try this simple experiment, by first looking at the hedges, &c., which he is rapidly passing, and then at some part of the interior of the carriage itself, especially one which presents a series of parallel lines. But when the impression of movement has been of longer duration, its effects are less transient; thus a person who has been for some time on board ship, sees the floors, walls, and ceilings of his apartments on shore in a state of continual up-and-down motion, even for some days after he has landed. This would seem to be rather a *sensorial* than a *retinal* phenomenon.

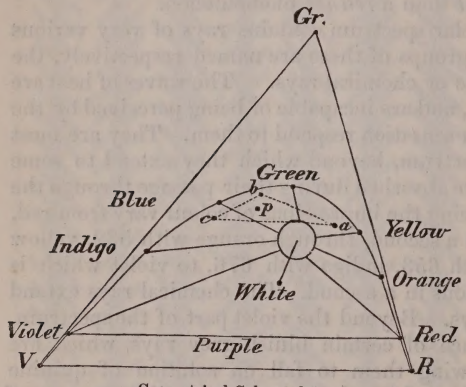
586. *Chromatoptometry.*—The solar spectrum contains rays of very various wave lengths or velocity, and three groups of these are named respectively, the calorific, the colorific, and the actinic or chemical rays. The waves of heat are longest, amounting to 0·00194 mm., and are incapable of being perceived by the retina, though the nerves of common sensation respond to them. They are most abundant at the red end of the spectrum, beyond which they extend to some distance, and 90 per cent. of them are absorbed during their passage through the media of the eye. The waves producing the impressions of colour vary from red, which has 481 billion vibrations in a second, through orange with 532, yellow with 563, green with 607, blue with 653, indigo with 676, to violet which is produced by 764 billions of vibrations in a second. The chemical rays extend some distance beyond the violet rays. Beyond the violet part of the spectrum, Helmholtz has observed the presence of certain bluish-grey rays, which are most easily demonstrated by allowing them to fall on solution of quinine sulphate, æsculin or petroleum, when they give rise to the phenomenon of fluorescence. The colorific rays are thus recognized by the number of their undulations in a second, and absorbed by the media of the eye about to the same extent as by water. The effects of the admixture of different colours may be investigated either by causing different colours from two solar or electric light spectra to fall on the same spot, or by looking obliquely through a glass plate at one colour whilst light of a different colour is reflected from the surface of the same plate, or by making a disk on which sectors of different colour are painted revolve rapidly, or lastly by looking, as in Scheiner's experiment, through two small holes separated from one another by a space less than the diameter of the pupil, and each of which is covered by a different coloured glass.† The three fundamental colours, as was originally shown by Thomas Young, are red, green and violet. The effects of a mixture of two simple but not complementary colours, is the same as that produced by the part of the spectrum which lies between them, after a certain amount of white light has been added to it. The less white that is combined with the mixture the more intense, or as it is sometimes termed, the more saturated is the tint of colour perceived. Hence the saturation of a colour

* A very beautiful "philosophical toy" was shown to the Author some years since, by its inventor, Mr. Roberts, the celebrated machinist of Manchester; consisting in an apparatus by which it was made possible to read words printed on a card, although the card itself was made to revolve on its axis even 40,000 times in a minute. The principle of its construction was simply this—that the eye caught a succession of glimpses of the card, through a narrow slit before which a disk with a single corresponding perforation was made to revolve; the rate of movement of this disk being so adjusted to that of the card, that whenever the eye caught sight of the latter, it was *momentarily* in the same position, so that, by the succession of transient impressions thus made upon the retina, the words printed on the card could be distinctly read.

† Landois, "Physiologie," 1880, p. 812.

diminishes with the intensity of the illumination under which it is seen. The accompanying diagram represents a geometrical colour plate, from which various conclusions can be drawn. In the centre is white, and from this point lines are drawn to the various points of the curve on which the names of the colours are described. Each would be most brightly illuminated towards the white end of the line, and most pure or saturated towards the opposite extremity. The effect of the mixture of two spectral colours may be obtained by drawing a straight line from the one point to the other; if then we suppose weights to hang from the two points of the curve indicating the position of the colours, and which weights shall represent the units of intensity of these colours, the position of the centre of gravities of the two in the line of junction will give the position in the plate of the mixed colour. Hence, the colour resulting from the mixture of two spectral colours, always lies on the straight line connecting the two colour points. Again, the complementary colour of a spectral colour may be immediately found if a line be drawn from the point of this colour through white, till it cuts the opposite part of the colour curve. The point where it cuts the colour curve shows the complementary colour. Lastly, the colour plate serves to discover the tint resulting from the admixture of three or more colours. Thus, for example, the effects of the admixture of the three colours, represented by the points *a* (pale yellow), *b* (nearly saturated greenish blue), and *c* (nearly saturated blue), may be determined by suspending weights from the three points which correspond to the intensity of each, and ascertaining the centre of gravity of the triangle *a b c*, which will lie at *p*. But this mixture of pale greenish blue, as may easily be seen can be also produced by the admixture of green blue with white, since *p* is also the centre of gravity of two weights which lie in the line joining white with green blue. The triangle *V Gr R* may also be drawn around the colour plate, and as the angles represent the three fundamental colours, red, green, and violet, it is obvious that every impression of colour that is in any point of the colour plate may be found if weights corresponding to the intensity of the fundamental colours be suspended from the angles of the triangle, for then the point of the colour table or the mixed colour, is the centre of gravity of the triangle thus weighted at its three angles. Each colour is perceived more distinctly in proportion to its *saturation*. By mingling it with white, its saturation may be diminished till at length it becomes invisible. Aubert* by experimenting with coloured pieces of paper placed on a rotating Maxwell's disk, finds that the limit of sensibility for a colour is reached when this is mixed with 120-180 parts of white. The influence of the *intensity* of a colour on its perceptibility is determined by mixing it with black, and Aubert† has shown that one part of colour on 359 parts of black is more than sufficient to produce a distinct impression of colour. As light fades into twilight and darkness, all colours become gre

Fig. 275.



Geometrical Colour plate.

* Aubert, "Physiologie der Netzhaut," p. 138. † Op. cit., p. 146.

in the following order: on a white ground, deep green, indigo, bright green, bright blue, red, yellow, and finally orange; on a black ground, deep green, brown, indigo, bright blue and bright green, red, yellow, and orange, which is thus always the last to be indistinguishable.* Colours which can no longer be distinguished when the eye is steadily fixed upon them, immediately re-appear when the position of the eye or of the coloured object is slightly altered. The retina is not equally susceptible to impressions of colour in all its parts.† It is only at the Fovea centralis, and the immediately adjoining part of the retina, that all shades of the primary colours can be clearly distinguished. The periphery of the retina is on the other hand insensitive to colour, all hues being only recognized as shades of which around the point of best vision in the centre of the retina‡ there is a zone where we perceive all of the so-called base colours, red, green, and violet. Outside of this is a zone in which green and violet are alone perceived, and beyond this another zone in which only blue or violet is perceived. Fick states§ that between the fovea and the periphery is an intermediate zone in which the sense of colour is imperfect, red, yellow, and green giving the impression of yellow, which is paler the greener the tint when seen in the polar zone, whilst blue and violet give the impression of blue, which is also paler, the nearer to green is the sensation produced when seen at the polar zone. The three zones named respectively the polar, the intermediate, and the peripheric zone, are by no means sharply defined from each other, and the influence of magnitude is considerable, the perception of the colour of a small object being much less accurate in the intermediate zone than that of a larger object.

587. When the Retina has been exposed for some time to a strong impression of some particular kind, it seems less susceptible of feebler impressions of the same kind. Thus, if we look at any brightly luminous object, and then turn our eyes on a sheet of white paper, we shall perceive a dark spot upon it; the portion of the retina which had been affected by the bright image, not being able to receive an impression from the fainter rays reflected by the paper. The dark spectrum does not at once disappear, but assumes different colours in succession—these being expressions of the states through which the retina is passing in its transition to the natural condition. If the eye has received a strong impression from a *coloured* object, the spectrum exhibits the *complementary* colour;‖ thus, if the eye be fixed for any length of time upon a bright red spot on a white ground, and be then suddenly turned so as to rest upon the white surface, we see a spectrum of a green colour. This, according to Helmholtz, is due to the fact that certain nervous elements destined to conduct impressions of red are fatigued; other elements, on the contrary, and especially those adapted to conduct impressions of green are at rest, but white light contains all colours, and green amongst the others, which, as the green-perceiving elements are not exhausted, are brought vividly into

* The experiments of Purkinje, Dove, and Grailich, are not in accord with those of Aubert, for they are of opinion that red is distinguished in twilight with greater difficultythan blue.

† Purkinje long ago stated that the periphery of the retina exhibits defective perception of different colours, red light appearing grey; yellow, green; green, bluish; whilst blue and violet are unaltered; and the recent investigations of Fick, "Arbeiten aus dem Physiol. Laborat. der Würzburger Hochschüle," 1878, Heft iv. p. 213. See also Holmgren, "Die Farbenblindheit," 1878; and Cohn, "Studien über Farbenblindheit," 1879.

‡ See Joy Jeffries' "Color Blindness."

§ "Physiol. Optik," Hermann's "Handbuch der Physiol.," Band iii. p. 206.

‖ By the 'complementary' colour is meant that which would be required to make white or colourless light, when mixed with the original: thus red is the complement of greenish blue (which may be made by mixing yellow and blue); blue is the complement of orange (red and yellow); and greenish yellow of purple (red and blue); and *vice versâ* in all instances.

view. In like manner each spectral colour can be rendered uncommonly vivid by previously exhausting the retina by gazing intently on its complementary colour.—The same explanation applies to the curious phenomenon of 'coloured shadows.' It may not unfrequently be observed at sunset, that, when the light of the sun acquires a bright orange colour from the clouds through which it passes, the shadows cast by it have a blue tint. Again, in a room with red curtains, the light which passes through these produces green shadows. In both instances, a strong impression of one colour is made on the general surface of the retina: and at any particular spots, therefore, at which the light is colourless but very faint, that colour is not perceived, its complement only being visible. The correctness of this explanation is proved by the fact, that, if the shadow be viewed through a tube, in such a manner that the coloured ground is excluded, it seems like an ordinary shadow. It is not unlikely that, as Müller suggests, the predominant action of one colour on the retina disturbs (as it were) the equilibrium of its condition, and excites in it a tendency to the development of a state corresponding to that which is produced by the impression of the complementary colour; for the latter is perceived, as he remarks, even where it does not exist; as when the eye, after receiving a strong impression from a coloured spot, and being directed upon a completely dark surface or into a dark cavity, still perceives the spectrum. This change, indeed, extends beyond the spot on which the impression is made (§ 592); for, as is well known to artists, the sensory impression producing any colour is greatly affected by neighbouring hues. Thus, if four strips of coloured paper, or any other fabric, A, B, C, D, —two of them, A, B, of one colour (*e.g.* red), and the other two, C, D, of some different colour (*e.g.* blue)—be laid side-by-side at intervals of about half an inch, the hues of the two central strips, B, C, will be decidedly modified by each other's proximity, each approximating to the hue of the complementary colour of the other; so that instead of

A	B	C	D
red	red	blue	blue,

we shall see

A	B	C	D
red	orange-red	greenish-blue	blue.

In the experiments of Mandelstamm,* it was found that the acuteness of perception of the eye for slightly different shades of colour was greatest in the yellow spectrum, and then successively less in the blue, green, indigo, and finally, in the red, in which it was least.† Lamansky‡ finds that the sensitiveness of the eye for colour is greatest in the order green, yellow, and blue, and least for red. In commencing atrophy of the optic nerve, red colour blindness first appears. Lamansky finds the time requisite for the perception of red three times greater than that for blue. Kunkel, however,§ states that the order of rapidity of perception is, red (0·0573 sec.), blue (0·0916 sec.), and green (0·133 sec.) The time requisite for distinct vision of a line is extremely brief. From experiments with the Electric Spark, O. N. Rood‖ estimates it for a black line at not more than four billionths of a second (0·000,000,868 sec., Landois). The means by which differences of colour are recognized are at present unknown. Young suggested that there might be

* "Archiv f. Ophthalmol.," Band xiii. Abtheil. ii. p. 399.

† A remarkable phenomenon of recurrent vision is described by Prof. Young in "Amer. Journ. of Sci.," vol. iii. No. 16.

‡ V. Gräfe's "Archiv," Band xvii. p. 123.

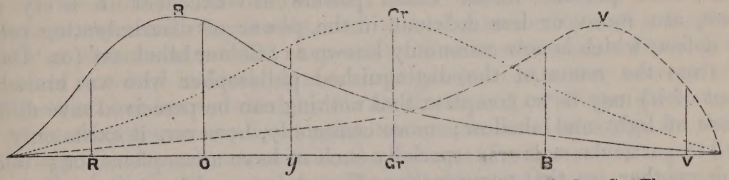
§ "Lond. Med. Record," 1874, p. 710.

‖ "American Journ. of Science and Art," ser. 3, vol. ii. p. 159.

different nerves, each having the power of discriminating one of the fundamental colours, but the structure of the retina gives no support to this view. The laminated structure observed by Max Schultze in the proximal extremities of the rods and cones may possibly have some relation to this power, for if the laminæ possessed a different refractive power in the several rods and cones, they would only transmit light of a certain colour.

588. To explain the mode in which light of various colours is perceived, it has been suggested that the Retina may contain three kinds of nerve termination, one of which when stimulated produces the sensation of red, a second of green, and a third of violet; the red perceiving elements are most strongly stimulated by the waves of greatest length in the spectrum; the green perceiving elements by those of medium length, and the violet perceiving elements by those of shortest length. At the same time it must be admitted

Fig. 276.



Distribution of colour in the Spectrum. R. The distribution of Red. Gr. The distribution of Green. V. The distribution of Violet.

that each colour of the spectrum stimulates all the elements, though some more feebly, and others more powerfully. Fig. 276 shows, by means of three curves, the mode in which the various sensations of colour may be produced. The continuous line represents red; the dotted line, green; the interrupted line, violet. Pure red as shown by the height of the ordinates stimulates the red perceiving elements of the retina strongly, the others more feebly, and the sensation perceived is red. Pure yellow stimulates the red and green perceiving elements moderately, the violet perceiving elements feebly, and the sensation produced is that of yellow. Pure green strongly stimulates the green perceiving elements, and much more feebly the two other kinds, giving the sensation of green, and so with the blue and violet. The sensation of a mixed colour results from the simultaneous stimulation of two kinds of elements, and if all are stimulated, the sensation of white light is experienced. As the recognition of colour is most acute at the fovea centralis, and as at this part there are no rods, but cones alone, it has been concluded that the perception of colour is a function of the cones and not of the rods. The latter would appear to possess only the power of appreciating quantitative variations in the amount of light.

589. The observations of Schultze seem to point clearly to the conclusion that the perception of colours is due to the cones and not to the rods, for not only is the fovea centralis of the human eye, where cones alone are present, the part most acutely sensitive to variations of colour, but in animals of nocturnal habits like the owl and the bat, no cones are discoverable, and we may conclude that vision in them is reduced to the quantitative perception of light; or, in other words, to the differences between shades of light and darkness. A simple experiment shows that our notions of colour are, like those of temperature, relative and not positive, for although, when a pair of smoked glasses are worn before the eyes, surrounding objects at first appear strongly tinged with their colour, very short experience enables the wearer to distinguish between different colours, and he sees, or seems to himself to

see, white objects of a fine white colour, until he undeceives himself by removing them.

590. Upon the properties of the Eye in regard to Colour are founded the laws of harmonious colouring, which have an obvious analogy with those of musical harmony. All complementary colours have an agreeable effect when judiciously disposed in combination; and all bright colours, which are not complementary, have a disagreeable effect, if they are predominant: this is especially the case in regard to the simple colours, strong combinations of any two of which, without any colour that is complementary to either of them, are extremely offensive. Painters who are ignorant of these laws, introduce a large quantity of dull grey into their pictures, in order to diminish the glaring effects which they would otherwise produce; but this benefit is obtained by a sacrifice of the vividness and force, which may be secured in combination with the richest harmony, by a proper attention to physiological principles.*

591. Some persons whose visual powers are excellent in every other respect, are more or less deficient in the power of discriminating *colours*. This defect, which is now commonly known as 'Colour blindness' (or 'Daltonism,' from the name of the distinguished philosopher who was himself the subject of it) may be so complete, that nothing can be perceived save different degrees of light and shadow; more commonly, however, it exists only with regard to particular colours, especially such as have a complementary relation to one another, so that persons thus affected are unable (*e.g.*) to distinguish ripe cherries among the leaves of the tree, save by their form; whilst in some individuals it does no more than confuse colours that are nearly related, such as green and blue, especially when they are seen by artificial light.† If we accept three fundamental colours, red, green, and violet, the failure to distinguish between these is termed partial colour-blindness, whilst inability to distinguish any colour at all is termed total colour-blindness. Holmgren has proposed that if the several shades of a given colour cannot be perceived, the condition should be termed complete, whilst if they can be distinguished, it should be called incomplete colour-blindness. In testing these conditions, a very requisite proceeding in signalmen, wools of various colour are placed before the patient. There are three kinds of colour-blindness, red blindness, green blindness, and violet blindness.‡ He who to a purple sample adds blue and violet strands, or either of these two, is red blind; but he who adds to the purple, green or grey or both, is green blind. The man who is violet blind adds to the purple, red and orange. A green sample may also be placed before the patient, because it is very easily confounded with grey. The very numerous examinations of school children in America by Joy Jeffries§ have shown that in that country 4·202 per cent. of boys

* This subject has been most carefully and elaborately investigated by M. Chevreul, whose recent Treatise on Colours has almost exhausted the inquiry into the mode in which the Visual sense of Man is affected by them. For a general view of the nature and attributes of Light, see Art. 'Light,' by Sir J. Herschel, in the last edition of the "Encyclopædia Metropolitana."

† See especially the Memoir of Prof. Seebeck, in Poggendorff's "Annalen," Band xlii. (1837); that of Prof. Wartmann, in "Taylor's Scientific Memoirs," vol. iv. p. 156; Mr. Pole's case recorded in the "Proceedings of the Royal Society," 1856–57, vol. viii. p. 172, and the interesting commentary upon it by Sir J. Herschel, in idem, vol. x. p. 72. See also Preyer, "Centralblatt," 1869, p. 72. A difference appears to exist between the effects of reflected and transmitted light in cases of colour-blindness. See Jeaffreson, "Lancet," 1872 ('Anerythropsia or true Daltonism'), pp. 601, 670. Clarke, idem, p. 635.

‡ See Michel, "Die Prüfung des Sehvermögens." München, 1878.

§ See 'Report in School Document,' No. 13, of the examination of 27,927 school children for colour-blindness, March, 1880.

are colour-blind, and only 0·066 per cent. of girls. Cohm* observed the same remarkable rarity of colour-blindness in women, and his average in males was 4 per cent. The proportion of cases of colour-blindness in Jews as compared with Christians in Breslau is as 4·8 : 3·6. Red blindness is by far the most common, constituting 80 per cent. of all cases. The ordinary form of colour-blindness seems to be only an extension of the want of perceptivity normal in the periphery of the Retina.†

592. The impressions made by luminous objects upon the Retina are not precisely confined to the spots upon which their rays impinge, but extend themselves to a greater or less distance around; which phenomenon has been termed *irradiation*. Thus if we make a circular white spot upon a black ground, and a black spot of precisely the same dimensions upon a white ground, the former will seem to be considerably larger than the latter; apparently because the excitation of the retina by the luminous impression tends to spread itself in each case over the adjacent non-excited space. Hence it is that we are able to distinguish any small magnitudes, such as letters or the lines of a diagram, at a much greater distance when they are marked in white on a black ground, than when inscribed in black upon a white ground. Another curious case of the same kind has been noticed by Sir D. Brewster.‡ "If we shut one eye, and direct the other to any fixed point, such as the head of a pin, we shall see indistinctly all other objects within the sphere of vision. Let one of these objects thus indistinctly seen, be a strip of white paper or a pen lying on a green cloth. Then, after a short time, the strip of paper, or the pen, will disappear altogether, as if it were entirely removed; the impression of the green cloth upon the surrounding parts of the retina, extending over that part of it which the image of the pen occupied. In a short time the vanished image will re-appear, and again vanish; when both eyes are open, the very same effect takes place, but not so readily as with one eye. If the object seen indistinctly is a black stripe on a white ground, it will vanish in a similar manner. When the object seen obliquely is luminous, such as a candle, it will never vanish entirely, until its light is much weakened by being placed at a great distance; but it swells and contracts, and is encircled by a nebulous halo."

593. The power of receiving and transmitting visual impressions is by no means uniformly diffused over the entire Retina. In the whole field of vision which at any time lies before us, we only see with perfect distinctness that part to which the axes of our eyes are directed, and of which the image, therefore, is formed upon the 'yellow spot.' Nevertheless we have a sufficiently distinct perception of the remainder of the field, to enable us to judge of the relations of the objects which are distinctly seen to those which surround them; and the mobility of our eyes enables us, under the guidance of our visual sense, to direct the most sensitive spot of the retina to

* "Studien üb. angeb. Farbenblindheit," 1879.

† For an interesting case in which the patient was affected with monocular green blindness and could yet see blue, though this colour, if it were a mixture of green and violet, ought to have appeared violet to him, see Preyer, "Centralblatt," 1872, No. 8; see also Lebert, "Klin. Monatschr. f. Augenheilk.," 1873, p. 867. The observations of Schelske (Gräfe's "Archiv," Band ix. Heft iii. p. 41) and Woinow (idem, Band xvi. Heft i. p. 200) have shown that the peripheral parts of the retina are, even in healthy persons, insensible to red, and perhaps to green, the latter colour being perceived as yellow. See also Rahlmann, Abst. in "Centralblatt," 1873, p. 357. Niemetschek, "Prag. Vierteljahrs.," Band c., 1868, p. 224, thought that in the colour-blind the distance between the eyes was abnormally small, and that this was due to imperfect development of the frontal convolutions, but this has been refuted by Holmgren, v. Gräfe's "Archiv," Band xxv. p. 135.

‡ 'Treatise on Optics,' in Lardner's "Cyclopædia," p. 296.

every part of the field in succession, not only without effort, but even almost without the consciousness that we are doing so.—Generally speaking, the indistinctness of vision for objects seen out of the axis of the eye, increases with the distance of their images from the central point; or, in other words, the impressibility of the several parts of the retina diminishes according to their distance from the 'yellow spot.' For a small space around it, however, the vision is tolerably accurate, and the extent of this circle or clear 'indirect vision,' as it is termed, varies in different people; Volkmann, for instance, can read an entire word by the light of a single electrical spark, and must therefore have instantaneously a direct and perfect perception of every part of it, whilst by others only a letter or two can be distinguished. It appears also from the experiments of Aubert and Förster,* and of Heymann,† that when the eye is accommodated for near objects, the limits of clear lateral perception are increased, or at least the perceptibility of that circle is intensified; so that of two objects which throw images of equal size on the retina, the smaller and more approximated one is distinctly perceived at a greater distance from the yellow spot than the larger and more distant object. But there is one part of the retinal surface—namely, the seat of entrance of the Optic Nerve, which is remarkable for its imperfect receptivity; as is shown by the following experiment. Let two black spots be made upon a piece of paper, about four or five inches apart; then let the left eye be closed, and the right eye be strongly fixed upon the left-hand spot; if the paper be then moved backwards and forwards, so as to change its distance from the eye, a point will be found at which the right-hand spot is no longer visible, though it is clearly seen when the paper is brought nearer or removed farther. In this position of the eye and the object, the rays from the right-hand spot cross to the nasal side of the globe, and fall upon the point of the retina which has just been mentioned. If the same experiment be tried with candles, the image will not entirely disappear, but will become a cloudy mass of light. It is not correct to say, as is sometimes done, that the retina is not impressible by light at this point; since, if such were the case, we should see a dark spot in our field of view whenever we use only one eye, which is not the case. The fact seems rather to be, that this portion of the retina is very inferior to the surrounding parts in its receptivity for luminous impressions; whilst, on the other hand, there is an unusual tendency to the extension of *their* condition to it by 'irradiation' (§ 592); so that, in the experiment just described, if the black spots be made upon a coloured ground, this colour will take the place of the spot which disappears.‡

594. That an electrical current is produced when light is allowed to fall upon the Retina, was first established by Holmgren.§ He observed an oscillation of the needle of the galvanometer under these circumstances in all vertebrates except Fishes. In the Frog the oscillation is positive, but in all others it is negative, but positive when the light is withdrawn; the yellow rays are the most active in this respect. The subject has been also taken up by Dewar and McKendrick,‖ who have corroborated and extended Holmgren's observations. The impression made by rays of light upon the Retina may be to a certain extent imitated by other physical agencies, which thus give rise

* "Archiv f. Ophthalmol.," Band iii. p. 1.

† "Acta Academ. C.L. C.G. Naturæ Curiosorum," Dresden, 1864.

‡ The diameter of the blind spot as obtained by experiment on the living eye is 1·55 mm. (Listing); 1·616 mm. (Hannover and Thomsen); 1·81 mm. (Helmholtz). The diameter of the optic disk, according to Weber, in the dead subject, varies from 2·10 mm. to 1·72 mm.

§ See Abstract in Humphry and Turner's "Journal of Anat. and Phys.," 1872, p. 225.

‖ See Humphry and Turner's "Journal of Anat. and Phys.," 1873, vol. vii. p. 275.

to various *subjective* visual phenomena. Advantage has recently been taken by Dr. Serre,* of the power of mechanical pressure to produce luminous spectra, for the investigation of the 'law of visual direction'; and the results which he has obtained are of very great interest. When any part of the globe of the eye is compressed (the experimenter being in a completely darkened room), a luminous figure is seen to be projected in the direction opposite to the spot pressed upon. Its form varies according to that of the compressing body, and to the degree in which the retina is affected by it. Thus if the pressure be made by the point of the finger, or by any other circular surface, upon a part of the globe over the interior of which the retina is continuous, the spectrum, or *phosphène* (as it is termed by Dr. Serre), is also circular ; if the compressing body, on the other hand, be square at its extremity, the 'phosphène' is also square ; and if it be triangular, the 'phosphène' is triangular too. But if the pressure be made near the anterior edge of the retina (which is what most commonly happens, unless the most favourable situation be designedly chosen), the figure of the 'phosphène' is incomplete ; and the degree of its deficiency corresponds with the proportion of the area of compression that does not lie over the retinal expansion. Hence there can be no hesitation in regarding the production of this spectrum as the immediate result of the affection of the sensorium by the pressure of the retina ; and as it seems to our perceptive consciousness to have a distinct objective existence, and as its position bears a constant and definite relation to that of the portion of the retina on which the impression is made, it seems obvious that any such affection of the retina not only immediately suggests to our minds the notion of an external objective cause of the impression, but also indicates to our consciousness the *direction* of the object.—But further, besides the principal 'phosphène,' another, of smaller dimensions, is usually to be seen, in a direction nearly the same as that on which the pressure is made ; this is the result of the transmission of the pressure to the *opposite* side of the globe, by an alteration of its figure and of the position of its contents, which corresponds to the fracture of the skull by *contre-coup*. The form of this smaller or secondary 'phosphène' is not affected by the cause which sometimes renders the larger or primary spectrum incomplete ; since, as we cannot anywhere apply pressure to the living Human eye, save on some part of its anterior hemisphere, the 'contre-coup' will always take place at the opposite spot in the posterior hemisphere, over which the retina is continuous, save at the entrance of the optic nerve. By an extensive series of observations upon the relation of the positions of the primary and secondary 'phosphènes,' both to each other and to the seat of compression, Dr. Serre has deduced the important conclusion, that the lines joining the imaginary spectra and the spots of the retina from whose affection they respectively proceed, pass through a common 'centre of direction,' whose position is in the middle of the crystalline lens. And hence it seems to be a legitimate conclusion, that our sense of the relative directions of external objects is derived from a kind of mental projection of each point of the retinal image, in the line which joins it to this 'centre of direction.'

595. Another very curious *subjective* phenomenon of Vision, is the representation which, under particular circumstances, we may mentally obtain of the retina itself; as in the following experiment, first devised by Purkinje, and known by his name. "If in a room otherwise dark, a lighted candle be moved to and fro, or in a circle, at a distance of six inches before the eyes, we perceive, after a short time, a dark arborescent figure ramifying over the

* See his "Essai sur les Phosphènes," Paris, 1853.

whole field of vision, this appearance is produced by the vasa centralia distributed over the retina, or by the parts of the retina covered by those vessels. There are, properly speaking, two arborescent figures, the trunks of which are not coincident, but on the contrary arise in the right and left divisions of the field, and immediately take opposite directions. One trunk belongs to each eye, but their branches intersect each other in the common field of vision. The explanation of this phenomenon is as follows:—By the movement of the candle to and fro, the light is made to act on the whole extent of the retina, and all the parts of the membrane which are not immediately covered by the vasa centralia are feebly illuminated; those parts, on the contrary, which are covered with these vessels, cannot be acted on by the light, and are perceived, therefore, as dark arborescent figures. These figures appear to lie before the eye, and to be suspended in the field of vision;"* and as the vessels appear magnified, and display a remarkable parallactic gliding movement over the visual field, data are afforded by which H. Müller has calculated that the true percipient surface of the retina must be situated at a certain distance from the vessels, corresponding in fact with the bacillar layer.† We have thus another demonstration of the fact, that, in ordinary Vision, the immediate object of our sensation is a definite condition of the retina, which is excited by the formation of a luminous image. The power of summoning up at will the visual representation of external objects, and especially of figures in the acts of mental calculation, the recollection of dates, and other mental processes, appears from the inquiries of Francis Galton,‡ who has applied the term 'visualization' to it, to be of not unfrequent occurrence. In such cases the figures arrange themselves in a series more or less irregular or interrupted in position—sometimes in vertical, at others in horizontal rows, certain numbers or groups of numbers being sometimes shaded or even coloured. This faculty seems to be more common in children than in adults.

596. The visual power is susceptible of extraordinary improvement, through the habitual direction of our *attention* to the effects produced upon our consciousness by the impressions transmitted to the Sensorium from the Eye; and this improvement may take place, either in regard to the quickness and readiness with which objects generally are perceived, or in the faculty of discriminating the slightest differences in form, shade, colour, &c., or of discerning bodies of extreme minuteness. In regard to all these points it may be noticed that the habit of attention to any particular class of objects, sharpens the discriminating power for that class alone; and that it is usually rather the mental than the corporeal vision which undergoes improvement. Thus the Seaman who makes out the 'loom of the land' where the landsman can discern nothing but an indefinite haze above the horizon, or who can distinguish the size, rig, and course of a vessel which the landsman can but just see as a formless speck, does so in virtue of the aptitude of his mind for receiving suggestions from minute indications such as pass unnoticed by those who have not been accustomed to form their ideas upon the same kind of experiences. And the Microscopist, who is constantly on the outlook for the various forms of organic structure with which his mind is familiar, discerns these without difficulty or hesitation, where an ordinary observer sees nothing

* Müller's "Elements of Physiology" (Baly's Translation), p. 1163.

† For the explanation of various other entoptical phenomena, see James Jago, B.A., in "Proceedings of the Royal Society," vol. viii. p. 603. He observes that the long beams of light which issue from flames regarded with 'winking eyes' proceed from little bars of fluid along the margins of the lids.

‡ See "Nature," vol. xxi. 1880, p. 252, *et seq.*

but a confused jumble of tissue. Extremely slight variations in the relative illumination of two objects can readily be discerned. According to Arago* the difference can be perceived when it amounts to no more than about 1-64th, according to Volkmann when it is from 1-60th to 1-100th, to Steinheil 1-38th, and to Masson 1-120th. Aubert† has shown that these variations in the results obtained by different observers are probably due to their having employed different amounts of illumination; since the perception of slight variations is much greater, within certain limits, with moderately bright than with feeble illuminating powers.—It is interesting to observe that the power of descrying objects at vast distances appears to be hereditarily possessed by two races of men, the Mongols of Northern Asia, and the Hottentots of Southern Africa, both of which habitually dwell on vast plains that seem to stretch without limit in every direction. It seems probable that this power was in the first instance acquired by habit in each case; and that, as frequently happens with acquired peculiarities which are kept up by constant use in successive generations,‡ it has become fixedly hereditary.

6. *Sense of Hearing.*

597. In the Ear, as in the Eye, the impressions made upon the sensory nerve are not at once produced by the body which originates the sensation; but they are propagated to it, through a medium capable of transmitting them. We obviously take cognizance by the mind, therefore, not of the sonorous object, but of the condition of the auditory nerve; and all the ideas we form of sounds, as to their nature, intensity, direction, &c., must be based upon the changes which they produce in it. The complex contrivances which we meet with in the organ of Hearing among higher animals, are evidently intended to give them greater power of discriminating sounds than is possessed by the lower tribes; in which last it is reduced to a form so simple that it may be questioned whether they can be said to possess an organ of *hearing*, if by this term we imply anything more than the mere consciousness of sonorous vibrations.—There is a considerable difference, however, between the Eye and the Ear, in regard to the special purposes for which they are respectively adapted. In the former we have seen that the whole object of the instrument is to direct the rays of light received by it, in such a manner as to occasion them to fall upon the expansion of the optic nerve in similar relative positions, and with corresponding proportional intensities, to those which they possessed when issuing from the object. We have no reason to believe anything of this kind to be the purpose of the Ear; indeed it would be inconsistent with the laws of the propagation of sound. Sonorous vibrations having the most various directions, and the most unequal rates of succession, are transmitted by all media without modification, however numerous their lines of intersection; and wherever these undulations fall upon the auditory nerve, they must cause the sensation of corresponding sounds. Still it is probable that some portions of the complex organ of hearing, in Man and in the higher animals, are more adapted than others to receive impressions of a particular character; and that thus we may be especially informed of the direction of a sound by one part of the organ, of its musical tone by another, and some other of its qualities by a third.

598. A single impulse communicated to the Auditory nerve through an appropriate apparatus, seems to be sufficient to excite the momentary sensation of *sound;* but most frequently a series of such impulses is concerned, there

* "Astronomie," vol. i. p. 194. † "Physiologie der Netzhaut," 1864.

‡ See "Princ. of Comp. Physiol.," § 620.

being but few sounds which do not partake, in a greater or less degree, of the character of a *tone*. Any continuous sound or tone is dependent upon a succession of impulses; and its acuteness or depth is governed by the rapidity with which these succeed one another. It is not difficult to ascertain by experiment, what number of such impulses or undulations are required to give every tone which the ear can appreciate. Thus if, as in the instrument termed the Syren, a circular plate with a number of apertures at regular intervals be made to revolve over the top of a pipe through which air is propelled, a succession of short *puffs* will be allowed to issue from this; and, if the revolution be sufficiently rapid, these impulses will unite into a definite tone. In the same manner, if a spring be fixed near the edge of a revolving toothed wheel, in such a manner as to be caught by every tooth as it passes, a succession of *clicks* will be heard; and these too, if the revolution of the wheel be sufficiently rapid, will produce a tone. The number of apertures in the plate which pass the orifice of the pipe in a given time, or the number of teeth which pass the spring, being known, it is easy to see that this must be the number of impulses required to produce the given tone. Each impulse produces a double vibration, forwards and backwards (as is seen when a string is put in vibration, by pulling it out of the straight line); hence the number of single vibrations is always double that of the impulses.—The maximum and minimum of the intervals of successive pulses, still appreciable by the ear as determinate musical sounds,* in persons endowed with an acute sense of hearing, may vary from 8 for the lowest, to above 40,000 for the highest note. Blake found that children of 12–13 years of age could perceive a note produced by 40,960 single vibrations at a distance of 34 feet. Young persons of 18–20 years heard the same only at a distance of 13–16 feet, but a note produced by 36,864 simple vibrations at 34 feet. Adults of 28–30 years could only hear at 34 feet a note produced by 32,768 vibrations. The deepest tone of orchestral instruments is the E of the Double Bass with $41\frac{1}{4}$ vibrations, the highest the d^v of the Piccolo flute with 4,752 vibrations (Tyndall). From the observations of Dr. Wollaston, it is evident that the ears of different individuals are differently constituted in this respect; some not being able to hear very acute tones produced by Insects, or even Birds, which are distinctly audible to others, whilst the same difference in the perception of low notes has been observed not only in different persons, but in the opposite ears of the same individual.† In regard to the precise time during which a sonorous impression remains upon the ear, it is difficult to procure exact information, since it departs more gradually than do visual impressions from the eye. This is certain, however—that it is much longer than the interval between the successive pulses in the production of tones; since it was found by M. Savart, that one or even several teeth might be removed from the toothed wheel, without a perceptible break in its sound—showing that, when the tone was once established, the impression of it remained during an intermission of some length. In Helmholtz's experiments it was observed that when the duration of each note in a succession of similar notes was less than 0·1 sec., the sound became continuous.

599. A very recondite investigation into the theory of Acoustics, and especially into the conditions on which the distinct qualities of musical tones

* Despretz, "Comptes Rendus," tom. xx. p. 1214. Hermann, "Grundriss der Physiologie," 1867, gives the limits at 40 and 16,000 double vibrations; Helmholtz at 16 and 38,000 single vibrations, or about 11 octaves. ("Boston Med. and Surg. Journ.," 1872, (vol. x. No. 20); Pfaundler ("Sitz. d. Wiener Akad.," Band lxxvi. 1877, p. 561) considers that only two beats in a second are required to produce an audible note.

† Högyes, "Medicin. Natur-wiss. Anzieger," 1879, p. 90.

depend, was undertaken by Helmholtz.* It is possible, he observes, to produce sounds consisting of only a single primary or *fundamental note;* the fundamental note of a sonorous body being the lowest tone which it yields when the whole of it is in vibration together; but in by far the greater number of instances, sounds, however produced, and whether musical in their character or not, are compounded of the fundamental note and a number of secondary, collateral, or harmonic notes; and the peculiar quality or *timbre* of particular instruments appears to be determined by a variation in the mode of grouping of the secondary sounds. Each such group Helmholtz designates a "sound colour." In a series of experiments upon the vowel sounds, *a*, *e*, *i*, *o*, and *u*, he has remarked that we distinguish them from one another† by the harmonic sounds which accompany the chief or fundamental note, and he endeavours to render this evident by the following experiments. He terms the fundamental note the first (1), whilst the harmonics (2, 3, 4, 5, 6, &c.) are notes produced by two, three, four, five, or six times the number of vibrations of the fundamental note. Thus, taking the middle C of the piano as the fundamental note, the harmonics will be C_2 (octave) G, C_3 (double octave) E_3 G_3, &c.

2 3 4 5 6

Now if the vowel *a* be sung close to a piano with the damper up, not only will the wire corresponding to the fundamental note be thrown into vibration, but also the wires corresponding to the 3rd and 5th harmonics, or those vibrating three times and five times as often as the fundamental note, and also more feebly the 2nd, 4th, and 7th harmonic notes. When the vowel *o* is sung, the 3rd harmonic note vibrates somewhat more weakly than when *a* is sung; the 2nd and 5th harmonics very weakly. With *u* the fundamental note vibrates almost alone; the 3rd harmonic very feebly. With *e* the wire of the 2nd harmonic is thrown into powerful vibration, but the higher harmonics are scarcely produced. With *i*, as with *u*, it is difficult to pronounce it loudly enough to excite vibrations in any but the fundamental note; the 2nd and 3rd harmonics, however, appear to aid in determining the clear character of the note, and slight vibrations may be observed in the 5th harmonic. The wires of the piano in these instances may be said to analyze the vocal sound into its secondary elements or partial notes; and Helmholtz has shown that the same result may be attained by placing in connection with the ear a series of glass vessels, producing by their vibration harmonic notes, and ascertaining with which note or kind of note they resonate most powerfully. In another series of experiments, instead of analyzing the vocal sounds as above mentioned, Helmholtz endeavoured to produce them *synthetically*, by accompanying a given fundamental note with its several harmonics. This was accomplished by a system of tuning-forks, arranged in harmonic series, which could be thrown into vibration at will in various order. Thus the fundamental note of the first tuning-fork, resembling the vowel *u*, the vowel sound or musical colour *o* was produced if the harmonics 2 were powerfully, and 3 and 4 were weakly, sounded; *e* was produced by the 3rd octave resonating powerfully with the fundamental note, the 2 harmonic note moderately, and the 4 and 5 harmonics feebly, and so on for the other vowel sounds. When two notes are simultaneously sounded, of which one is higher than the other, if the higher note be some multiple of the lower, being produced by 2, 3, 4, or 6 times as many vibrations, harmony is produced; but if the two sounds do not stand in such relation to each other, interference phenomena are pro-

* "Die Lehre von den Ton-empfindungen als physiologische Grundlage für die Theorie der Musik," Braunschweig, 1862.

† It must be borne in mind that the *German* pronunciation of the vowels is here implied.

duced, producing alternate augmentation and diminution of the sound, which are perceived as 'beats.' The number of the beats is of course always equal to the difference in the number of vibrations of the two sounds Thus, if one note has thirty-three vibrations in a second, and another has thirty-four, one beat will be heard every second. If the lower note has sixty-six and the higher sixty-eight vibrations in the second, there will be two beats in the second, and so on. The slighter the difference between the two notes, the more infrequent will be the beats. If a considerable interval of time intervene between two beats, they are perceived to be distinct; but if this occur more rapidly, they produce a painful sensation of discord, which reaches its maximum when there are thirty-three beats in one second, which occurs when the number of vibrations of one note is 528 and of the other 495 per second. Beyond this number the sensation of discord diminishes.—From what has been stated above it appears that the power which we possess of distinguishing the characters belonging to similar notes produced by different instruments, is due to a kind of analysis being performed by the ear, similar to that effected by the wires of the piano; and we shall see that it is not unreasonable to attribute this function especially to the branches of the auditory nerve distributed upon the lamina spiralis of the cochlea. It may be said, indeed, to have received direct confirmation from the observations of Hensen* upon the auditory hairs on the free surface of a Decapod Crustacean (Mysis). These were seen under the microscope to vibrate in certain groups corresponding with the special note sounded in their vicinity. In the case of the human ear a very effective 'damping apparatus' must exist, since through the greater part of the musical scale a trill of ten alternate notes in the second can be distinctly differentiated, which would be confused if the sensation of each note persisted much longer than the sound itself.

Fig. 277.

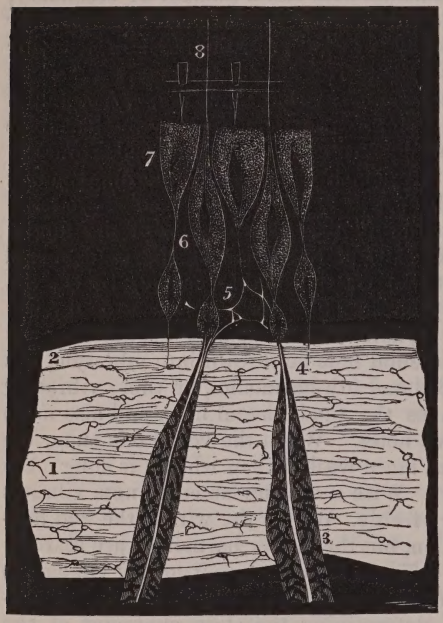


Diagram of the mode of termination of the auditory nerve in the ampullæ and sacculi. 1, Cartilage of the wall of the ampulla. 2, Structureless basement membrane. 3, Doubly contoured nerve fibre. 4, Axis-cylinder traversing the basement membrane. 5, Plexiform union of fine nerve fibres with interspersed nuclei. 6, Fusiform cells with nucleus and dark fibre in their interior. 7, Supporting cells. 8, Auditory hairs.

600. The essential part of an Organ of Hearing is obviously a nerve endowed with the peculiar property of receiving sonorous undulations, and of transmitting their effects to the Sensorium. This nerve is spread out over the surface of a delicate membrane which lines the Vestibule and its prolongations; and this membrane encloses a fluid, which is the medium whereby the sonorous vibrations received through the external ear are communicated to the nerve.† We learn from an examination of the comparative

* "Zeits. f. wiss. Zoologie," Band xiii.; and "Kieler Institut.," 1869.

J. Horbaczewski (Wiener, "Acad. Sitz.," Band lxxi. p. 312) finds that in the sheep the

structure of the auditory apparatus in the lower animals, and from the study of its development in the higher, that the part which, being most constantly present, and being also the earliest in its development, may be considered as the most essential, is the simple *Vestibular* cavity; which exists where there are no vestiges either of Semicircular Canals, of Cochlea, or of Tympanic apparatus. Such a condition presents itself in some of the higher Invertebrata and in the lowest Fishes; but as we ascend the Vertebrate series, we find the semicircular canals growing out (as it were) of the Vestibule in Fishes, a Tympanic apparatus superadded in Reptiles, and a Cochlea first acquiring a more than rudimentary development in the class of Birds, although only presenting in Mammalia that characteristic form from which it derives its name.* In regard to the mode in which the ultimate subdivisions of the Auditory nerve are distributed upon the lining membrane of the labyrinth, the observations of Rüdinger, Urban Pritchard, and others have demonstrated that the area of distribution of the auditory nerve in the vestibule and semicircular canals is limited to five spots of yellowish colour, visible respectively in the sacculus, the utriculus, and the three ampullæ. In the latter the area of distribution is raised into a kind of ridge or crest (crista acustica of Schultze), whilst in the sacculus and utriculus it is merely an oval spot, which has received the name of the *macula acustica*. At these spots the membranous labyrinth is firmly adherent by a layer of dense connective tissue to the bony wall, not being separated from it by the perilymph. The membrane presents three layers: an external layer of loose connective tissue; a denser layer, named the tunica propria; and lastly, a single layer of epithelial cells. At the macula the loose outer layer is lost, becoming blended with the periosteum, which in many animals here present branched pigment cells. The tunica propria remains unchanged. The tesselated cells increase in thickness, becoming first cuboid and then columnar, and finally over the surface of the macula becoming changed into nerve epithelium. The arrangement of the nerve epithelium presents the following peculiarities. (See Fig. 277.) There is a row of two alternating forms of elongated cells, bordered by a distinct cuticular membrane, and each having a superficial and a deep nucleus. One of these forms is named by Dr. Pritchard the "thorn cell," and the other the "bristle cell." The *thorn cells* have a fusiform body, containing an oval nucleus; a tapering cilium passes upwards from the cell body and projects through an opening in the cuticular membrane; the lower tapering extremity of the body passing downwards again expands, and encloses a second nucleus. The *bristle cells* have a triangular body, containing an oval nucleus; the base of the cell is intimately connected with the cuticular membrane, and from this base passes upwards a single narrow cilium or bristle, having parallel and non-tapering borders. The apex of the body is prolonged downwards, and has a second enlargement, containing a second oval nucleus, usually situated at a different level from that of the corresponding enlargement of the thorn cell. The cuticular membrane is thick, and serves to keep the cell-elements in

vestibular and cochlear nerves are quite distinct from each other at their origin; the fibres of the cochlear nerve are always much finer than those of the vestibular. In the sheep the distribution of the two nerves is sharply limited to the parts after which they are named, but they are much less so in man and the horse. In man the various roots form a common trunk which in the first instance divides into a nerve for the vestibule, and a nerve for the cochlea; the latter, however, is not distributed exclusively to the cochlea, but gives off a fine branch which runs in the recessus cochlearis to the vestibular end of the ductus cochlearis, and through the macula cribrosa quarta to the septum of the two sacculi contained in the vestibule.

* For a more detailed sketch of the Comparative Anatomy of the Organ of Hearing, see the Author's "Principles of Comparative Physiology," §§ 711–714.

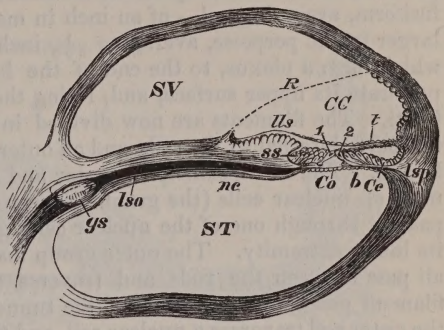
place. As it resembles the reticulate membrane of the organ of Corti, it may also be distinguished by the same name—the *membrana reticularis*. Towards the margin of the macula the cells and their various parts elongate, and pass by insensible gradations into the columnar form of the epithelial cells which surround it. Near the centre of the macula, the upper nucleus and surrounding protoplasm of the bristle cells gradually diminish and are ultimately lost, the cell being represented by a trabecula from the membrana reticularis tapering towards its second or lower nucleus. The bristle remains after the upper protoplasmic mass has disappeared, but eventually this also is lost. The trunk and branches of the vestibular division of the portio mollis contains large fusiform bipolar ganglion cells corresponding to those of the ganglion spirale of the cochlea. On arriving at the membrana propria, the nerve fibres lose their white substance and enter the nerve epithelium without it. They here form a plexus around the deep layer of nuclei, and some of the filaments may be traced directly or indirectly into the ciliated cells. Covering the acoustic spot is the 'otolith mass,' a soft mass of cuticular tissue into which the cilia project. It is analogous to the membrana tectoria of the cochlea. The otoliths are fixed by this mass, and are chiefly contained in its outer portion. The structure of the cochlea has been materially elucidated by the extraordinarily minute and delicate dissections of Corti,* Pritchard, and others. It presents two chambers in section, an upper or scala vestibuli (*SV*, Fig. 278), and a lower or scala tympani (*ST*, Fig. 278), separated from each other by the lamina spiralis. The scala vestibuli is subdivided by the membrane of Reissner (*R*) into the scala vestibuli proper and the canalis cochleæ (*CC*). The proximal part of the lamina spiralis is composed of a bony plate, united on both sides with periosteum. It terminates externally or peripherally by a grooved border, formed of a modification of connective tissue, the upper toothed edge of which is named the *limbus*. Beyond the attachment of the membrane of Reissner, the lamina spiralis is continued to the opposite wall of the cochlea by the *membrana basilaris*, which is prolonged from the lower lip of the limbus, and it is on this membrane that the organ of Corti is situated. The organ of Corti, which is the essential part of cochlea and is represented in Fig. 279,† is situated partly on the lower lip of the limbus or terminal portion of the bony lamina spiralis and partly on the membrana basilaris. It is bounded on both sides by epithelium. It consists of :—1. The rods of Corti; 2. The ciliated or hair cells; 3. Certain nuclear cells; 4. The supporting cells; 5. The membrana reticularis; and 6. The membrana tectoria. The rods of Corti are arranged in two rows, an inner and an outer, with their upper extremities in close contact, but separated by a considerable interval below, so that the two rows sloping towards each other form the roof of a triangular tunnel. The foot of the inner rod stands on the lower lip of the limbus, and that of the outer on the membrana basilaris.

* See his Memoir in Kölliker and Siebold's "Zeits. für wiss. Zoologie," 1851, Band iii. Heft 1; also Prof. Kölliker's "Mikroskop. Anatomie," Band ii. § 289, and his "Manual of Microscopic Anatomy," 1860; Fick, "Anat. u. Physiol. der Sinnes-Organe," 1862, p. 122. Rüdinger, "Das Gehör-organe," München, 1867, with an Atlas of Photographs; Reichert, "Abhand. d. k. Akad. der wiss. zu Berlin;" C. Hasse, 'On the Mode of Termination of the Acoustic Nerves in Birds,' in the "Göttingen Nachrichten," 1867, and Kölliker's "Zeits.," Band xvii. p. 598. Pritchard, in "Monthly Microscop. Journ.," 1873, vol. ix. p. 150, and "Quart. Journ. Mic. Sci.," Oct. 1876; A. V. Winiwarter, "Wien. Akad. Sitz.-ber.," Band lxi. Abth. 1; and Abstract in "Centralblatt," 1870, p. 853; Gottstein, "Centralblatt," 1870, p. 625, and 1872, p. 385; and Rüdinger and Waldeyer, in Stricker's "Hum. and Comp. Histology," Syd. Soc. Trans., 1873, vol. iii.; Kühn, "Archiv. f. Mik. Anat.," Band xiv. p. 264.

† From a drawing by Urban Pritchard in the "Proceed. Roy. Soc.," No. 168, 1876.

The outer surface of the head of the inner rod is hollowed for the reception of the head of the outer rod, and a long process is given off which runs outwards. On either side of the rods are situated various cells; above, and closely adherent to them, is the *membrana reticularis*, and above this is the thick *membrana tectoria*. The length of the rods is graduated, and ranges from 1-150th of an inch at the apex of the spiral to 1-500th inch at its base, the length of the outer rods increasing more rapidly than that of the inner. The *hair cells* are very delicate, columnar in form, with large round nuclei and nucleoli; the rest of their contents is finely granular. From each of their flat summits a row of four bristles or cilia project. There are four rows of hair cells—one (*e*, Fig. 279) situated internally to the rods, the other three (*f*) externally to them. The lower ends of the hair cells are evenly rounded off, and the summits are attached to the membrana reticularis, through the rounded apertures of which the bristles project. The *nuclear* cells have no cell-walls, and are directly connected with nerve filaments. They are found first on the lower lip of the sulcus internal to the rods, in a mass of three irregular layers constituting the 'granular layer' of Waldeyer; secondly, arranged in three or four rows below the level of the outer hair cells, constituting the 'cells of Deiters;' thirdly, there is one in each lower angle of the triangular tunnel formed by the rods of Corti; and lastly, there are one or two scattered about. The '*supporting cells*' of Hensen form the outer boundary of the organ. They are oval or columnar in form, and Pritchard describes one or two similar cells forming the inner boundary of the organ, and names them the inner supporting cells. They form a link between the hair cells and the epithelium. The *membrana reticularis* is composed of a fibrous network, which, on the inner side of the rods, presents one row of regular circular openings, through which the bristles of the inner hair cells project. Over the rods it presents long meshes, and over the outer hair cells there are two forms of meshes—the one elongated, called a *phalanx*, the other circular, called an *annulus*, so arranged that each phalanx is surrounded by four annuli. Through the annuli the bristles of the outer hair cells project. Connected with the membrana reticularis are three rows of fibrous cords, situated on the outer side of each row of the outer hair cells. These trabeculæ pass down to the membrana basilaris. The *membrana tectoria*, or membrane of Corti, is a mucous mass secreted from the epithelial cells, and therefore soft in the fresh state. It commences at the attachment of the membrane of Reissner to the limbus, and passes over the teeth of the limbus as a layer of equal thickness. Then becoming much thicker, it covers the organ, and gradually tapers off externally into the thin general layer which lines the rest of the ductus cochleæ. The bristles of the hair cells penetrate into this mass. The organ of Corti is not found at the two

Fig. 278.



Section through one of the coils of the *cochlea*:—S T, scala tympani; S V, scala vestibuli; C C, canalis cochleæ; R, membrane of Reissner, consisting of a single layer of nucleated flattened cells, extending from just behind the teeth of the limbus to the upper part of the ligament of the cochlea; *lls* to *lsp*, lamina spiralis membranacea; *lls*, limbus laminæ spiralis; *ss*, sulcus spiralis; *gs*, ganglion spirale seated on *ne*, the nervus cochlearis indicated by the black line; *lso*, lamina spiralis ossea; *l*, membrana tectoria; *b*, membrana basilaris; C *o*, organ of Corti; *lsp*, ligamentum spirale; C *c*, cells of Claudius; 1, proximal rod of Corti; 2, distal rod of Corti.

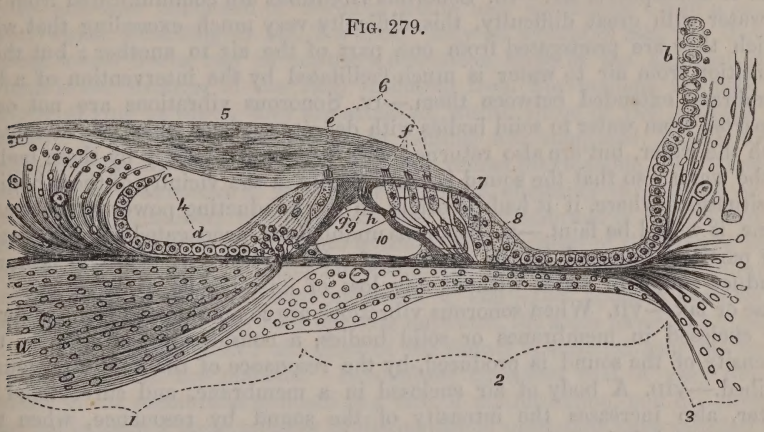
extremities of the lamina spiralis. The whole organ and its chief component parts, as the rods of Corti and hair cells, enlarge in proceeding from base to apex. The cochlear nerve in the substance of the modiolus, in passing upwards, gives off branches at right angles, which traverse a spiral ganglionic mass, the ganglion spirale, and then enter the lamina spiralis. This ganglion is situated in the lamina at the base, and gradually becoming more central in position, is found entirely in the modiolus at the apex; its cells are bipolar and fusiform, averaging $\frac{1}{1000}$ of an inch in man and most mammals, but are much larger in the porpoise, averaging $\frac{1}{600}$ inch. The nerve-fibres run in bundles, which form a plexus, to the end of the lower lip of the limbus, where they perforate its upper surface, and, losing their dark borders, reach the organ of Corti. The filaments are now divided into two groups—an inner, passing to the parts internal to the rods, and an outer, passing to the opposite side of those bodies. The inner principally enter and appear to terminate in the adjacent mass of nuclear cells (the granular layer of Waldeyer); one large filament, passing through one of the nuclear cells, goes to the inner hair cell and enters its lower extremity. The outer group may be divided into three sets, which all pass between the rods and traverse the triangular tunnel. The upper filament passes along the roof of the tunnel, and on reaching the other side of the outer rod traverses a nuclear cell, and then passes on to the first of the outer hair cells. The middle filament traverses the centre of the tunnel and enters the same nuclear cell, besides sending a branch downwards to another of the nuclear cells. The third or lower filament runs along the floor of the tunnel, being connected with the two nuclear cells in the lower angles of it; on the outer side of the rods this filament enters the nuclear cell, which has received the descending branch from the middle filament: and this cell, again, is connected with the first cell of Deiters by another filament. Filaments in the form of festoons connect the hair cells with each other, and analogous nervous connections are found between the cells of Deiters. A highly educated musical ear is able, according to Weber, to distinguish a sixty-fourth of a semitone, and as in each of the seven octaves which constitute the limits of hearing there are twelve semitones, the total number of intervals perceptible by a cultivated ear is 5,376. But the number of the arches of Corti is estimated by Kölliker at 3,000 (3,500 outer rods, 5,250 inner rods, Pritchard), with at least two radial fibres for each arch. The number of radial fibres is therefore more than sufficient to enable the keyboard of the cochlea to respond by a special cord to each of the sounds that experience has demonstrated to constitute the scale of the most highly-endowed musicians.*

601. In order to gain any definite idea of the uses of different parts of the Ear, it is necessary to bear in mind that sounds may be propagated amongst solid or fluid bodies in three ways; by *reciprocation*, by *resonance*, and by *conduction*.—1. Vibrations of *reciprocation* are excited in a sounding body, when it is capable of yielding a musical tone of definite pitch, and another body of the same pitch is made to sound near it. Thus if two strings of the same length and tension be placed alongside of each other, and one of them be sounded with a violin-bow, the other will be thrown into reciprocal vibration; or if the same tone be produced near the string in any other manner, as by a flute or a tuning-fork, the same effect will result.—2. Vibrations of *resonance* are of somewhat the same character; but they occur when a sounding body is placed in connection with any other, of which one or more parts may be thrown into reciprocal vibration; even though the tone of the whole be different, or it be not capable of producing a definite

* See M. Duval, "Nouveau Dictionnaire de Médecine," t. xxv. p. 452.

tone at all. This is the case, for example, when a tuning-fork in vibration is placed upon a sound-board; for even though the whole board have no definite fundamental note, it will divide itself into a number of parts, which will reciprocate the original sound, so as greatly to increase its intensity; and the same sound-board will act equally well for tuning-forks of several different degrees of pitch. When a smaller body is used for resonance, however, it is essential that there should be a relation between its fundamental note

FIG. 279.



A typical section through the lamina spiralis membranacea. 1. Limbus (*a*) nerve; 2. Lamina spiralis membranacea; 3. Ligament of cochlea, (*b*) stria vascularis; 4. Sulcus spiralis (*c*) upper, (*d*) lower lip; 5. Membrana tectoria; 6. Hair cells of Corti (*e*) inner, (*f*) outer; 7. Membrana reticularis in section; 8. Supporting cells (Hensen); 9. Rods of Corti (*g*) inner, (*h*) outer; 10. Triangular ligament.

and that of the sonorous body; otherwise no distinct resonance is produced. Thus, if a tuning-fork in vibration be held over a column of air in a tube, of such a length that the same note would be given by its vibration, its sound will be reciprocated. And if it be held over a pipe, the column of air in which is a multiple of this, the column will divide itself into that number of shorter parts, each of which will reciprocate the original sound, and the total action will be one of resonance. But if the length of the pipe bear no such correspondence with the note sounded by the tuning-fork, no resonance is given by the column of air it contains.—3. Vibrations of *conduction* are the only ones by which sounds can strictly be said to be propagated: these are distinguishable into various kinds, into which it is not requisite here to inquire. It should be remarked, however, that all media, fluid, liquid, or solid, are capable of transmitting sound in this manner; a vacuum being the only space through which it cannot pass. The transmission is usually much more rapid through solid bodies than through liquid; and through liquid than through gaseous. The greatest diminution in the intensity of sound is usually perceived when a change takes place in the medium through which it is propagated, especially from the aëriform to the liquid.

602. The detailed application of these principles has been most elaborately worked out by Professor Müller; and the following statement is little more than an abstract of the results of his experimental investigations; of which the first series bears specially on the case of those animals which, living immersed in water, receive the sonorous undulations through that medium. The labyrinth of such as possess a distinct organ of hearing, is either entirely enclosed within the bones of the head, as in the Cephalopoda and in the Cyclostome and Osseous Fishes; or, its cavity being prolonged to the surface

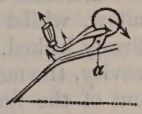
of the body, it is there brought into communication with the conducting medium by means of a membrane, besides receiving the vibrations through the medium of the solids of the body, as is the case in Cartilaginous Fishes and Crustacea:—I. Sonorous vibrations, excited in water, are imparted with considerable intensity to solid bodies.—II. Sonorous vibrations of solid bodies are communicated with greater intensity to other solid bodies brought in contact with them than to water; but with much greater intensity to water than to atmospheric air.—III. Sonorous vibrations are communicated from air to water with great difficulty, this difficulty very much exceeding that with which they are propagated from one part of the air to another; but their transition from air to water is much facilitated by the intervention of a lax membrane extended between them.—IV. Sonorous vibrations are not only imparted from water to solid bodies with definite surfaces which are in contact with the water, but are also returned with increased intensity by these bodies to the water; so that the sound is heard loudly in the vicinity of those bodies, in situations where, if it had its origin in the conducting power of the water alone, it would be faint.—V. Sonorous undulations, propagated through water, are partially reflected by the surfaces of solid bodies.—VI. Thin membranes conduct sound in water without any loss of its intensity, whether they be tense or lax.—VII. When sonorous vibrations are communicated from water to air enclosed in membranes or solid bodies, a considerable increase in the intensity of the sound is produced, by the resonance of the air thus circumscribed.—VIII. A body of air enclosed in a membrane, and surrounded by water, also increases the intensity of the sound by resonance, when the sonorous undulations are communicated to it by a solid body.

603. Animals living in air are nearly always provided with an opening into the vestibule, the *fenestra ovalis*, covered by a thin membrane; and generally with a *Tympanic apparatus* also. The following experimental results bear upon the manner in which the Ear of such animals is affected by sound.—IX. Sonorous undulations, in passing from air directly into water, suffer a considerable diminution in their strength; while, on the contrary, if a tense membrane exist between the air and the water, the sonorous undulations are communicated from the former to the latter medium with great intensity.—X. The sonorous vibrations are also communicated without any perceptible loss of intensity from the air to the water, when, to the membrane forming the medium of communication, there is attached a short solid body, which occupies the greater part of its surface, and is alone in contact with the water.—XI. A small solid body, fixed in an opening by means of a border of membrane, so as to be moveable, communicates sonorous vibrations from air on one side to water or the fluid of the labyrinth on the other, much better than solid media not so constructed. But the propagation of sound to the fluid is rendered much more perfect if the solid conductor, thus occupying the opening, is by its other end fixed to the middle of the tense membrane which has atmospheric air on both sides.—The fact stated in IX. is evidently one of great importance in the physiology of hearing; and fully explains the nature of the process in those animals which receive the sonorous vibrations through air, but which have no tympanic apparatus. In X. we have the elucidation of the action of the fenestra ovalis, and of the moveable plate of the stapes which occupies it, in animals living in air but destitute of tympanic apparatus; this is naturally the case in many Amphibia; and it may happen as the result of disease in the Human subject. In XI. we have a very interesting demonstration of the purpose and action of the tympanum, in the more perfect forms of the auditory apparatus.—We are now prepared to inquire, in somewhat more

of detail, into the actions of the different parts of this apparatus; and it will be better to commence with those of the *Middle* and *Internal Ear*, the accessory organs being afterwards considered.

604. The *Membrana Tympani* consists of three layers; an *external* one continuous with the cutis of the external meatus, and consisting of dermoid tissue with a covering of epidermic cells; an *internal*, which is extremely thin, continuous in like manner with the mucous membrane lining the tympanic cavity, and also composed of dermoid tissue and epithelium; and a *middle* layer, which, according to Mr. Toynbee,* may be separated into two distinct laminæ whose fibres run in contrary directions, those of the external layer (which is the stronger of the two) *radiating* from the malleus towards the peripheral ring to which they are attached, whilst those of the internal are *annular*. The fibres of which these laminæ are composed appear to be tendinous; and the membrane as a whole is almost inextensible. Mr. Toynbee points out the existence of a tubular ligament, enclosing the tendon of the tensor tympani muscle; and considers that the membrane is maintained by this ligament in a state of moderate tension, the assistance of the muscle being only required to augment this.—The membrane is usually inserted so obliquely that the plane of the two forms an angle of 125°–138° opening downwards. Each is funnel-shaped, the base opening outwards, the sides having an inclination of 125° to each other; the apex of the funnel is attached near the centre to the handle of the malleus. Bounafont† considers that a very oblique position of the membrana tympani is a vice of conformation, and his observations made upon a large number of distinguished musicians have satisfied him that in those whose ears are highly developed or sensitive, the tympanum is placed nearly vertically, its whole surface thus presenting itself for the reception of sounds. The function of the *Membrana Tympani* seems obviously to be the reception of sonorous undulations from the air, in such a manner that it may be thrown by them into a reciprocal vibration, which is communicated to the chain of bones, and, as is shown in the accompanying little diagram, through them to the membrane of the fenestra ovalis. Helmholtz has shown that the curvature of the membrana tympani, whilst it diminishes the amplitude of the vibrations, increases their force. In its usual state, this membrane is scarcely on the stretch; and this is found by experiment to be, for a small membrane, the best condition for the propagation of ordinary undulations. This is easily rendered sensible in one's own person; for an increased tension may be given to the membrana tympani either by holding the breath and forcing air into the Eustachian tube, so as to distend it from within, or by exhausting the cavity, so as to cause the external air to make increased pressure upon it; and in either case the hearing is immediately found to become indistinct. It is observed, however, that grave and acute sounds are not equally affected by this action; for the experimenter renders himself deaf to grave sounds, whilst acute sounds are heard even more distinctly than before. This fact is readily understood by referring to the laws of Acoustics already mentioned.‡ The greater the tension to which the membrana tympani is subjected, the more acute will be its fundamental tone; and as no proper reciprocation can take place in it to any sound *lower* than its fundamental tone, its power of repeating perfectly the vibrations proper to the deeper notes will

Fig. 280.



* "Philosophical Transactions," 1851. See also Moldenhaver, "Entwicklung des Mittleren und äussern Gehörgangs." † "Maladies des Oreilles," 1873, p. 278.

‡ See the Experiments of Schapringer ("Wien. Akad. Sitz.-ber.," Band lxii. 1870), who possessed the faculty of voluntarily contracting his tensor tympani.

diminish. The nearer a sound approaches to the fundamental note proper to the tense membrane, the more distinctly will it be heard. On the other hand, when the membrane is in its naturally relaxed condition, its fundamental note is very low, and it is capable of repeating a much greater variety of sounds; for, when it receives undulations of a higher tone than those to which the whole membrane would reciprocate, it divides itself into distinct segments of vibration, which are separated by lines of rest; and every one of these reciprocates the sound,* at the same time rendering it more intense by multiplication (§ 601). These facts enable us to understand the influence of the *tensor tympani* muscle in augmenting the tension of the membrane, and thus enabling it to vibrate in reciprocation to sounds having a great variety of fundamental notes. It appears to be antagonized by the *stapedius*, the contraction of which seems to diminish the tension of the membrana tympani, and to take off pressure from the fluid of the labyrinth. These two muscles conjointly may be considered to regulate the transmission of sonorous undulations to the fluid of the internal sac, preventing it from being too violently affected by loud sounds, in the same manner that the iris regulates the admission of light to the eye (§ 575); and the analogy extends also to their nervous supply, the stapedius being excited to action by a branch of the Facial, whilst the tensor tympani receives its nerves from the Optic ganglion.† They are probably put into conjoint action when we are *listening* for faint sounds, so as to bring the tympanum into the state of tension best adapted to reciprocate them: whilst by a like preparation, the concussive effects of a loud sound that is *anticipated*, are more effectually moderated than when it strikes the ear without warning. It is probably owing to an imperfect action of these muscles, that some persons are deaf to grave sounds, whilst they readily hear the more acute. Helmholtz‡ observes, that by the transference of the vibrations of the tympanum to the much smaller membrane of the fenestra ovalis, mechanical power is gained for the establishment of vibrations in the comparatively incompressible fluid of the labyrinth. He observes also that the inferior aspects of the articular surfaces of the malleus and incus are furnished with small teeth, so arranged that when the malleus moves outwards the articular surfaces easily separate as far as the somewhat loose capsule will allow, whilst when the malleus moves inwards these two bones become firmly locked. The result of this is, that when air is blown into the tympanic cavity, the membrana tympani can move outwards without dragging the stapes out of the fenestra ovalis. Neither the integrity of the membrana tympani

* This is very easily proved by experiment on a membrane stretched over a resonant cavity; for if light sand be strewed upon it, and a strong musical tone be produced in its vicinity, the membrane will immediately be set in vibration, not as a whole (unless its fundamental note be in unison with that sounded), but in different segments, of which every one reciprocates the sound; from the vibrating parts the sand will be violently thrown off, but it will settle on the intermediate lines of rest, which are known as the *nodal* lines, forming a variety of curious figures. See also Donders on the sound colours of the vowels in Donders and Berlius, "Archiv f. d. Holland. Beiträge zur Natur und Heilkunde," Band iii. p. 446. By means of a modification of Scott's form of König's phonautograph, Donders obtained very beautiful pictures or series of curves, representing complicated vibrations, not only of the vocals, but also of the notes produced by the passage of these into consonants, of the sound colours of various musical instruments, and of various notes—all of which present curves of appropriate form. See also Tyndall's work "On Sound," 1867, for a full résumé of all recent researches, and Squire on 'The Quality of Musical Sounds,' "Quart. Journ. of Sci.," 1865, p. 600.

† See Mr. C. Brooke in "Lancet," 1843, p. 380; and Mr. Toynbee in "Brit. and For. Med.-Chir. Rev.," vol. xi. p. 235.

‡ 'Ueber die Mechanik der Gehörknöchenchen,' Pflüger's "Archiv," 1868. See Humphry and Turner's "Journal of Anatomy," vol. iii. 1868, p. 219; also Buck, "New York Med. Journ.," June, 1874.

nor of the chain of ossicles is essential for hearing. It is sufficient that the stapes, and the membrane occupying the fenestra ovalis should be uninjured. All clinical observation shows that the detachment of the stapes, and the rupture of the membrane of the fenestra ovalis, or the ankylosis of the stapes to the margins of the opening rendering it immovable, abolishes hearing so far as this is dependent on the vibrations of the outer air.*

605. The uses of the *Tympanic Cavity* are very obvious. One of its purposes is to render the vibrations of the membrane quite free; and the other, to isolate the chain of bones in such a manner as to prevent their vibrations from being weakened by diffusion through the surrounding solid parts. As to the objects of the *Eustachian Tube*, opinions have been much divided. Many of these opinions, however,—such as the one most commonly entertained, that it serves the same purpose as the hole in an ordinary drum, removing an impediment to the free vibration of the membrane that would be offered by the complete enclosure of the air within,—are at once negatived by the fact, which seems to have been demonstrated by Mr. Toynbee and Dr. Jago,† that the guttural orifice of the tube is usually *closed*, being only opened during the act of swallowing.‡ The principal object of the Eustachian tube (which is always found where there is a tympanic cavity) seems to be the maintenance of equilibrium between the air within the tympanum and the external air. Dr. Jago indeed holds that the normally closed condition is a provision against the ingress of aërial undulations from the throat, which, if admitted, would threaten the membrana tympani with incessant oscillations, and that as the moment seized for bringing the tympanum into communication with the fauces must be one in which there can be no respiratory current, the period selected is the instant of swallowing, at which instant there is a compulsory suspension of respiration; so that neither shouting, singing, whistling, nor coughing can be performed.§ It also has the office of conveying-away mucus secreted in the cavity of the tympanum, by means of the vibratile cilia which clothe its lining membrane; and the deafness consequent on occlusion of this tube, is in part explicable by the accumulation which then takes place in the cavity. From what has been stated, it is evident that sonorous undulations in the air will be propagated to the fluid contained in the labyrinth—through the tympanum, the chain of bones,‖ and

* The increase in the resonance of the voice, and the greater distinctness with which a tuning-fork is heard when the external auditory meatus is plugged with the finger or with wax, is attributable in part to the slight condensation of the air in the meatus that is thus produced (Gellé, "Soc. de Biologie," 1877; "Tribune Medicale," 1877, p. 67), and in part to the obstacle to the escape outwards of the sonorous vibrations (Hinton).

† See his very interesting essays in the "Med.-Chir. Review," 1867, pp. 175 and 496.

‡ Loc. cit., and "Proceedings of the Royal Society," 1852.

§ Lucæ ("Archiv f. Ohrenheilk.," Band iii. p. 186) maintains that exchange of air in the tympanum takes place during the ordinary acts of respiration, and that it is *not* limited to the instant of swallowing. See Zuckerkandl, 'Zur Anat. u. Physiol. der Tuba Eustachiana,' "Monatssch. f. Ohrenheilk.," Dec. 1873, and Knapp's "Archives of Ophth. and Otol.," 1874, vol. iv. No. 1, p. 126. Poorten, "Monats. f. Ohren. Heilkund," 1874, p. 27, observed a case in which the Eustachian tube was kept patent by cicatrices, and in which the patient experienced a very disagreeable resonance of his own voice.

‖ For papers showing that sounds are chiefly conducted through the bones of the tympanum, see J. Jago, in "Proceedings of Royal Society," 1857–59, vol. ix. p. 134; and J. Toynbee, in idem, 1859–60, vol. x. p. 32. See also on this point Dr. Gustav Brunnen on 'The Connection between the Ossicles of Hearing,' in Knapp's "Archives of Ophthalmology and Otology," vol. iii. No. 2, p. 145, and Burnett, "Monthly Journal of Aural Surgery," July, 1871; Politzer, "Archiv f. Ohrenheilk.," Band iv. Heft 1. Buck, however (Hinton's 'Report on Otology,' "Med.-Chir. Rev.," April, 1873, p. 489), found on measuring with a micrometer the little lines into which starch granules scattered over the ossicula are thrown, that the vibrations of the malleus are twice as large as those of the incus, and four times as large as

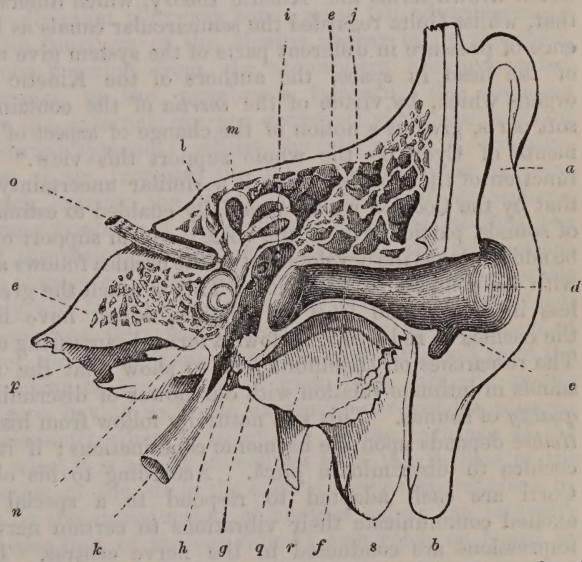
the membrane of the *fenestra ovalis* to which the stapes is attached—without any loss, but rather an increase of intensity. It is of great importance, as Dr. Jago has shown, that the external surface of the membrana tympani should be clean and free from moisture, since if it be rendered moist the power of hearing is immediately lessened; and since its inner surface is continually moist, an additional argument is furnished for the view that sonorous undulations are chiefly conveyed through the ossicula, and not through the air contained in the tympanum. Why water should be chosen as the medium through which the impression is to be made upon the nerve, it is impossible for us to say with anything like certainty, in our present state of ignorance, as to the physical character of that impression. But the problem being to communicate to water the sonorous undulations of air, the experimental results already detailed satisfactorily prove that—whilst this may be accomplished, in a degree sufficient for the wants of the inferior animals, by the simple interposition of a membrane between the air and the fluid—the tympanic apparatus of the higher classes is most admirably adapted for this purpose. The fenestra ovalis is not, however, the only channel of communication between the tympanum and the labyrinth; for there is in most animals a second aperture, the *fenestra rotunda*, leading into the cochlea, and simply covered with a membrane. It is generally supposed that, the labyrinth being filled with a nearly incompressible fluid, this second aperture is necessary to allow the free vibration of that fluid, the membrane of the fenestra rotunda being made to bulge-out, as that of the fenestra ovalis is pushed-in. It may be easily shown by experiment, however, as well as by reference to comparative anatomy, that no such contrivance is necessary; for sonorous undulations may be excited in a non-elastic fluid, completely enclosed within solid walls at every part, except where these are replaced by the membrane through which the vibrations are propagated; and this is precisely the condition, not only of Invertebrate animals, but even of Frogs; in which last a tympanic apparatus exists, without a second orifice into the labyrinth. Moreover it is certain that the vibrations of the air in the cavity of the tympanum must of themselves act upon the membrane of the fenestra rotunda; and this is perhaps the most direct manner in which the fluid in the cochlea will be affected, although it will ultimately be thrown into much more powerful action, by the transmission of vibrations from the vestibule. For it has been satisfactorily determined by experiment that vibrations are transmitted with very much greater intensity to water, when a tense membrane, and a chain of insulated solid bodies capable of free movement, are successively the conducting media, than when the media of communication between the vibrating air and the water are the same tense membrane, air, and a second membrane:—or, to apply this fact to the organ of hearing, the same vibrations of the air act upon the fluid of the labyrinth with much greater intensity, through the medium of the chain

those of the stapes; hence the intensity of the sound waves appears to undergo diminution on their passage from the membrana tympani to the labyrinth. Politzer employed an instrument he named the Tympanograph, fixing fine filaments of glass to each of the bones and recording their movements on a revolving drum. His experiments showed that the amplitude of the vibrations of the several bones was equal, and that, contrary to what might have been expected, the interrupted nature of the chain did not diminish the intensity of the sound waves. Mr. Brooke's observation is also worthy of notice, that, inasmuch as the rapidity of conduction of sound differs considerably in solids and aëriform fluids, if sound were conducted by both means to the labyrinth, confusion would result. The views of Muller, admitting waves of condensation and rarefaction, are supported, in part at least, by Hensen and Schmidekan ("Untersuch. d. Kinder. Instituts," 1869) and Henke ("Zeits. f. rat. Med.," Band xxxi.), who fastened glass threads to the ossicula, and observed great variation in the amplitude of the vibrations, which were sometimes vertical and sometimes transverse.

of auditory bones and the fenestra ovalis, than through the medium of the air of the tympanum and the membrane closing the fenestra rotunda, which last, it is maintained by Dr. Jago, has little if any influence in the transmission of sounds to the internal Ear.—The fenestra rotunda is not to be considered as having any peculiar relation with the cochlea; since, in the Turtle tribe, the former exists without the latter.

606. It is obviously in the *Labyrinth* as a whole, that the sonorous vibrations are brought to bear upon the Auditory nerve spread out to receive them. In regard to the special functions of particular parts of the labyrinth, however, no certainty can be said to exist. The membrane which lines its cavities not only contains a liquid (the *endo-lymph*, *Scarpa's tumour*), but is also separated from the osseous wall by another collection of liquid, the *peri-lymph* or *liquor Cotunnii*; so that it is suspended, as it were, in a liquid which bathes both its surfaces. In the cavity of the Vestibule, which is subdivided by a membranous partition into two, are small round masses of concretionary particles, collectively named *otoconia*, or ear-powder; these are obviously the rudiments of the *otoliths*, or ear-stones, whose presence, in animals with a less perfect auditory apparatus, seems needful to intensify the undulations. —It was formerly supposed that the *Semicircular Canals* had for their peculiar function, to receive the impressions by which we distinguish the *direction* of sounds; and it is certainly a powerful argument in support of this view, that, in almost every instance in which these parts exist at all, they hold the same relative positions as in Man, their three planes being nearly at right angles to one another; but it is now no longer held, because it can be easily shown that the direction of sounds cannot be estimated except by two or more simultaneous or consecutive observations. If a sound of moderate intensity be made at a point equidistant from the two ears, we are unable to judge of its position unless we are aided by the visual sense—and the difficulty of indicating accurately the position of a cricket or deathtic, is well known. The curious movements witnessed by M. Flourens* after section of one or more of these canals (§ 480),

Fig. 281.



Vertical Section of the *Human Ear*, the internal portions on an enlarged scale:—*a*, *b*, *c*, external ear; *d*, entrance to auditory canal, *f*; *e*, *e*, petrous portion of temporal bone; *g*, membrana tympani; *h*, cavity of the tympanum, the chain of bones being removed; *i*, openings from this cavity into the cells, *j*, excavated in the bone; on the side opposite the membrana tympani are seen the fenestra ovalis and rotunda; *k*, Eustachian tube; *l*, vestibule; *m*, semicircular canals; *n*, cochlea; *o*, auditory nerve; *p*, canal for carotid artery; *q*, part of glenoid fossa; *r*, styloid process; *s*, mastoid process.

* See Cyon's 'Researches on the Ear,' in "Nature," 1878, Oct. 10, with Crum Brown's criticisms upon them.

to which reference has already been made, have led to another theory of their use. Flourens observed that section of a membranous canal was always followed by movements of the head or even of the body of the animal in the direction of the divided canal, and hinted that they were concerned in the co-ordination of movements. This suggestion was elaborated by Goltz into what has been termed the statical theory, namely—that the termination of the nerves in the ampullæ, may be supposed to be stimulated by pressure or by stretching. The endo-lymph necessarily presses most upon that part of the wall of the canal which is situated at the lowest point, and each position of the head will correspond to a particular distribution of pressure, and therefore, to a particular form of nerve stimulation. We have thus a special sensation corresponding to each position of the head. The importance of a knowledge of the position of the head and control over its movements in preserving the equilibrium of the body was shown by Goltz, who fixed the head of a pigeon in an unnatural position, when it was found to be incapable of flying, and walked with difficulty. Mach, Breuer, and Brown have advanced a theory which Crum Brown terms the 'Kinetic' theory, which differs from that of Goltz, in that, whilst Goltz regarded the semicircular canals as organs which by difference of pressure in different parts of the system give us a notion of the aspect of the head in space, the authors of the Kinetic theory regard them as organs which, by virtue of the *inertia* of the contained liquid and movable soft parts, give us a notion of the change of aspect of the head. The experiments of Cyon on the whole support this view.* Regarding the special function of the *Cochlea*, there is a similar uncertainty. It has been surmised that by the Cochlea we are especially enabled to estimate the *pitch* and quality of sounds, particularly of the voice; and in support of this idea the fact may be adduced that the development of the cochlea follows a very similar proportion with the compass of the voice. This is much the greatest in the Mammalia; less in Birds; and least in Reptiles, which have little true vocal power: the cochlea is reduced to its lowest form, disappearing entirely in the Amphibia. The researches of Helmholtz tend to show that the function of the cochlea stands in intimate relation with our power of discriminating differences in the *quality* of sounds. This will naturally follow from his demonstration that the *timbre* depends upon the harmonic combinations; if it be the function of the cochlea to discriminate *pitch*. According to his observations, the rods of Corti are each adapted to respond to a special tone, and when thus excited communicate their vibrations to certain nerve fibres, by which the impressions are conducted to the nerve centres. The individual branches of the auditory nerve are probably only capable of distinguishing simple, pendulum-like vibrations, but, as already stated (§ 599), all ordinary sounds are compound in their nature, the fundamental note being accompanied by harmonics; these throw corresponding fibres into vibration, and produce an impression which may be likened to a colour. The analogy which exists between the power of distinguishing *colours* and that of discriminating musical *tones* has long been recognized; and whilst we find that some persons are endowed with the latter, which is commonly known as a 'musical ear,' in a degree that renders it a source of great discomfort to them (since every discordant sound is a positive torment), others are altogether destitute of it—the deficiency being very analogous to the 'colour-blindness' formerly described. It is not a little curious that the two defects are occasionally

* Though he records an important one that is opposed to it, namely, that rabbits, after complete division of the auditory nerve, presented after rotation the same symptoms of vertigo as were exhibited by normal rabbits.

co-existent in the same individual.* The chief objection to Helmholtz's theory is that there are no rods in the cochlea of Birds. Hensen suggests that the radial fibres of the membrana basilaris are primarily thrown into vibration, and it is possible that the hairs of the hair cells, being of various length, may also respond to particular notes.

607. We have now to consider the functions of the accessory parts—the *External Ear*, and the *Meatus*. The Cartilage of the external ear may propagate sonorous vibrations in two ways; by reflection, and by conduction. In reflection, the concha is the most important part, since it directs the reflected undulations towards the tragus, whence they are thrown into the auditory passage. The other inequalities of the external ear cannot promote hearing by reflection; and the purpose of the extension of its cartilage is evidently to receive the sonorous vibrations from the air, and to conduct them to its source of attachment. In this point of view the inequalities become of importance; for those elevations and depressions upon which the undulations fall perpendicularly, will be affected by them in the most intense degree; and in consequence of the varied form and position of these inequalities, sonorous undulations, in whatever direction they may come, must fall advantageously upon some of them.—The functions of the Meatus appear to be threefold. The sonorous undulations entering from the atmosphere are propagated directly, without dispersion, to the membrana tympani: the sonorous undulations received on the external ear are conveyed along the walls of the meatus to the membrani tympani: whilst the air which it contains, like all insulated masses of air, increases the intensity of sounds by resonance. That in ordinary hearing, the direct transmission of atmospheric vibrations to the membrana tympani is the principal means of exciting the reciprocal vibrations of the latter, is sufficiently evident; the undulations which directly enter the passage will pass straight on to the membrane; while those that enter obliquely will be reflected from side to side, and at last will fall obliquely on the membrane, thus perhaps contributing to the notion of direction. The power of the lining of the meatus to conduct sound from the external ear, is made evident by the fact that, when both ears are closely stopped, the sound of a pipe having its lower extremity covered by a membrane, is heard more distinctly when it is applied to the cartilage of the external ear itself, than when it is placed in contact with the surface of the head. The resonant action of the air in the tube is easily demonstrated by lengthening the passage by the introduction of another tube; the intensity of external sounds, and also that of the individual's own voice, as heard by himself, is then much increased.

608. Many facts prove, however, that the fluid of the Labyrinth may be thrown into vibration in other ways than by the Tympanic apparatus. Thus in Osseous Fishes, it is only by the vibrations transmitted through the bones of the head, that hearing can take place. There are many persons, again, who can distinctly hear sounds which are thus transmitted to them; although, through some imperfection of the tympanic apparatus, they are almost insensible to those which they receive in the ordinary way. It is evident, where this is the case, that the nerve must be in a state fully capable of functional activity; and on the other hand, where sounds cannot thus be perceived, there will be good reason to believe that the nerve is diseased. Urbantschitsch† finds that there are three deaf-spots in each ear, or spots in which a vibrating

* See a collection of such cases, by Dr. Pliny Earle, in "Amer. Journ. of Med. Sci.," vol. xxxv. See also Ladovsky, "Archiv f. Mik. Anat." Band xxxiii. p. 497.

† "Centralblatt f. d. Med. Wiss.," 1872, No. 3.

tuning-fork passed in front of the ear is not heard. The two chief areas have the form of two little triangles, one of which extends forwards and upwards, the other backwards and upwards.

609. The power of distinguishing the *direction* of sounds appears to be, in Man at least, for the most part acquired by habit; for it is sometime before the infant seems to know anything of the direction of noises which attract his attention. Our judgment as to this point is probably assisted, in most cases, by a difference in the intensity of the sensations received through the two ears respectively; but since we have a certain power of appreciating direction when one ear alone is used, this power must depend upon an exercise of perceptive discrimination (which is probably acquired, rather than intuitive) in regard to the impressions which we receive through its means; and it has been already mentioned that the Semicircular canals (§ 606) appear to furnish the instrumentality by which our minds are enabled to take cognizance of such differences.—The idea of the *distance* of the sonorous body is another acquired perception, depending principally upon the loudness or faintness of the sound, when we have no other indications to guide us. In this respect there is a great similarity between the perception of the distance of an object, through the Eye by its size, and through the Ear by the intensity of its sound. When we are acquainted with the usual intensity of its sound, we can judge of its distance; and *vice versâ*, when we know its distance, we can at once form an idea of its real strength of tone from that with which our ears are impressed. In this manner the mind may be affected with corresponding deceptions through both senses: for as, in the Phantasmagoria, the figure being gradually diminished while its distance remains the same, it appears to the spectators to recede (the illusion being more complete if its brightness be at the same time diminished); so the effect of a distant full military band gradually approaching may be alike given by a corresponding *crescendo* of concealed instruments. It is upon the complete imitation of the conditions which govern our ideas of the intensity and direction, as well as of the character, of sounds, that the deceptions of the Ventriloquist are founded. A very curious instance of the degree in which our auditory interpretation is affected by other sense perceptions is afforded by the 'Ghost' exhibition which has recently been so popular; for it is scarcely possible to avoid referring to the place where they *seem* to be made, sounds which are really produced elsewhere.

610. The Auditory sense, like the visual, may vary considerably among different individuals, both as regards its general acuteness, and as respects its discriminative power for particular classes of impressions. Much depends upon the *habit of attention* to its indications; and thus it comes to pass, that the power of hearing very faint sounds and of recognizing their source becomes augmented to a wonderful degree in those individuals who are obliged to trust to the knowledge thus acquired for the direction of their own actions; whilst, in like manner, the power of distinguishing slight differences in the pitch of sounds may be so cultivated (where it is not congenitally deficient) as to attain an intensity that seems very extraordinary to those who have not accustomed themselves to listen for them. The general cultivation of this sense is perhaps most remarkable in blind persons, who have enabled themselves, by reliance upon it, to walk about freely, even in the crowded thoroughfares of the metropolis; and who are not only able to judge of the habits of individuals whom they meet by the sound of their footsteps (at once recognizing, for instance, the footstep of a policeman on duty), but can even tell when they are passing a stationary object (such as a lamp-post, provided it be as high as the ear or nearly so, by the reverberation of the sound of

their own footsteps, and can discriminate between a lamp-post and a man standing still in the position of one, by the same means.* The effect of habitual attention in increasing the discriminative power for impressions of one particular kind, is perhaps best seen in the ability which is possessed by certain Conductors of orchestral performances, to detect the slightest departure from time or pitch in the sound of any one of (perhaps) a hundred instruments that are simultaneously sounding, and to fix without hesitation upon the faulty instrumentalist. Seebeck, indeed, affirms that accomplished musicians can detect a difference in pitch between two sounds which only differ by 1-1200th in the number of their vibrations.† According to the researches of MM. Renz and Wolff,‡ our faculty of estimating differences in the *intensity* of sounds is much less perfect. When the intensities of two sounds are to one another as 7 to 10, the difference can be distinguished, but not when they are in the relation of 9 to 10. The advantage resulting from the simultaneous employment of the two ears in distinguishing minute differences in the intensity and pitch of sounds, is well shown in the experiment suggested by M. Weber, of holding two watches in the hand before one ear, when it will be found that the successive sounds can be distinctly heard, though they cannot be distinguished one from the other, whilst if one be held in front of each ear the two sounds can be clearly discriminated.

611. Facts of much interest have been ascertained, some of which have been already alluded to (478), in regard to an occasional difference in the rapidity of the perception of sensory impressions received through the Eye and through the Ear respectively. These facts are the result of comparisons made amongst different Astronomical observers, who may be watching the same visual phenomenon, and 'timing' their observations by the same clock: for it has been remarked, that some persons see the same occurrence a third or even a half of a second *earlier* than others. There is no reason to suppose from this, however, that there is any difference in the rate of transmission of the sensory impressions in the two nerves. The fact seems rather to be, that the Sensorium does not readily perceive two impressions of different kinds with equal distinctness; and that, when several such impressions are made on the senses at the same time, the mind takes cognizance of one only, or perceives them in succession. When, therefore, both sight and hearing are directed simultaneously to two objects, the communication of the impression through one sense will necessarily precede that made by the other. The interval between the two sensations is greater in some persons than in others; for some can receive and be conscious of many impressions, seemingly at the same moment; whilst in others a perceptible space must elapse. The 'personal equation' of each observer in an Observatory has, therefore, to be determined and allowed for.§

* See the account of a blind boot-lace-seller given by Mr. H. Mayhew in his "London Labour and the London Poor," vol. i. p. 402.

† See Ludwig, "Physiologie," vol. i. p. 380; and Béclard, "Physiol.," 1862, p. 1858.

‡ "Archiv f. Phys. Heilk.," 1856.

§ In all the best Observatories, an arrangement is now made for recording observations which supersedes the necessity of timing them by simultaneous attention to the clock. The observer who is watching the transit of a star (for example) across the meridian, simply presses a button at the moment when he witnesses its contact with the cross-wire. This pressure breaks an electric circuit, which is so connected with a chronometer as to stop it instantaneously, and thus automatically to record the precise time of the phenomenon. Since this plan has been adopted, it has been found that the "personal equation" nearly or altogether disappears; thus confirming the view given above as to its dependence on the distraction of the attention between the two objects of perception. For interesting papers on the subject of this paragraph, see Mach, 'On the Sense of Time in the Ear,' Moleschott's "Unters," Band x. 1866, Heft 2. Also Mach, 'On the Accommodation of the Ear,' in idem, p. 201.

612. Amongst other important offices of the sense of Hearing is that of supplying the sensations by which the Voice is regulated. It is well known that those who are born entirely deaf, are also dumb; that is, they do not spontaneously or imitatively form articulate sounds, though not the least defect may exist in their organs of voice. Hence it appears that the vocal muscles are usually guided in their action by the sensations received through the Ears, in the same manner as other muscles are guided by the sensations received through themselves; but when the former are deficient, the action of the vocal muscles may be guided by the latter (§ 496).—That the perceptions obtained by the auditory nerve should be capable of being more quickly perceived and registered than those received through the optic is not surprising, since the course of the former is much shorter than that of the latter. The following Table gives the results of several observers in regard to the physiological time of the several senses of sight, hearing, and touch; or in other words the whole term occupied between the occurrence of an event and its registration :—

	For vision.	For hearing.	For common sensation.
Hirsch . . .	0·2	0·149	0·182 hand.
Hankel . . .	0·2057	0·1505	0·1548 ,,
Donders . . .	0·188	0·18	0·154 neck.
Wittich* . .	0·194	0·182	0·1301 forehead.

By subtracting the physiological time for auditory impressions from those for optical impressions, it appears that the rapidity of the conduction of sensory impulses is comparatively slow. On the highest estimate not exceeding 7·35 metres per second, and on the lowest amounting to only 1·068 metres per second.

The Measure of Sensations.—The observations made by Weber and others on the several senses, have led to the establishment by Fechner of a psycho-physical law† applicable to the quantitative sensations of temperature, pressure, muscular exertion, sound, light, and of fatigue. At first sight it would seem impossible to measure a sensation, but inasmuch as the excitation of any nerve which leads to sensation is caused by external or physical conditions which we can vary or quantitatively determine, we possess in this a means of measuring sensations. Thus, if a weight of half an ounce be held in the hand, and another half ounce be added, a difference is instantly felt; but the addition of half an ounce to twenty pounds is not appreciated. The same is true of light and sound. It would hence appear that for an excitation to be felt, it must be proportionately more feeble as the excitation to which it is added is feeble, and stronger in proportion to the strength of the original or primary excitation. Hence the conclusion may be drawn that the intensity of a sensation increases, not directly in proportion to the intensity of the excitation that produces it, but in some other ratio. Now it may be asked, what proportion does the increase in the intensity of the sensation bear to the increase in the intensity of the stimulus? And in order to acquire this knowledge, three methods of experimentation have been adopted, named by Fechner respectively the method of the *smallest perceptible differences*, the method of *true and false estimates*, and the method of *mean error*. The *first method* consists in this:—Two weights, A and B, are to be compared. If they are nearly alike, they may be judged to be equal; if the difference be considerable it will easily be recognized. If the difference d between A and B be gradually increased or gradually diminished, a point will be arrived at when the difference is only just discernible, and the smaller the difference perceptible, the more acute is the sensibility of the subject. The *second method* consists in taking two weights, the difference between which is so small that an error in judgment is possible. In proportion as the difference increases, the number of accurate conclusions will augment at the expense of the inaccurate ones. If the total number of experiments be 100, and the number of true estimates be 70, we have the

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* See Von Wittich's Paper in Henle and Meissner's "Zeitschrift," 1868, Band xxxi. p. 87.

† Fechner, "Elemente der Psychophysik." 2 vols. Leipsic, 1860. Delbœuf, "Recherches Théoriques et Expérimentales sur la Mesure des Sensations," Bruxelles, 1873. Ribot, 'La Psychologie Physiologique en Allemagne,' in "La Rev. Scient.," No. 24, 1874. This section is chiefly drawn from Wundt, "Physiologie," 1873.

proportion $\frac{70}{100}$ established by the comparison of the two weights A and B. Now suppose a weight *a* to be given, we seek to determine the weight *b*, which compared with *a* will give the same proportion of $\frac{70}{100}$. Cases of indecision must be placed half to the account of the true and half to the account of the false estimate. The *third method* consists in taking a weight, A, exactly determined by balance, and it is sought by the judgment alone to fix on another weight which is judged equal to the first. In general the second weight differs from the first by a quantity, *d*, which is small in proportion to the acuteness of the sensibility of the subject. This experiment is frequently repeated, the positive and negative errors added, the signs being neglected. The total is divided by the number of trials, and the mean error is thus obtained. By the employment of one or other of these methods the following results are obtained :—

Sensation of Weight.—The hand is extended and supported, the eyes are bandaged, and successive weights, as a drachm, an ounce, a pound, &c., are placed upon it. On each weight various small additional weights are placed till a distinct difference is perceived. The results of numerous experiments by the first method have shown that a very simple relation is maintained—viz., that whatever may be the weight originally placed on the hand, it requires an addition of one-third of that weight to enable a distinct difference to be perceived.

Sensation of Muscular Effort.—This is a much more delicate means of estimating differences of weight than the foregoing, since not only does the sense of pressure, but the sense of muscular effort guide the judgment; and experiments have shown that an additional weight of 6-100th can be detected—*i.e.*, a weight of 6 grains added to 100 grains, or of 60 grains to 1000 is perceptible.

The *Sensation of Temperature* seems to follow the same law as that of simple pressure without muscular exertion, an addition of one-third being requisite to be perceived. In regard to light, photometrical experiments have shown that the intensity of a candle or other source of light must be increased 1-100th in order that the increase should be perceptible. For the sensation of sound, the increase or diminution must be equal to one-third. Renz and Wolff found that for two sounds to be clearly distinguished, they must be in the relation of 100 : 72. The proportion given by Volkmann is 4 : 3, which equal 100 : 75.

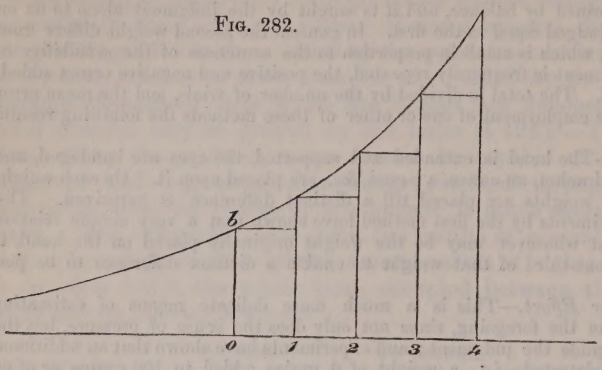
From all this it would appear that if S represent the value of the minimum perceptible sensation, the second possible sensation would be for tactile impressions $S+\frac{1}{3}$; for muscular effort, $S+\frac{1}{17}$; for temperature, $S+\frac{1}{3}$; for light, $S+\frac{1}{100}$; for sound, $S+\frac{1}{3}$; and the results of numerous experiments are as follow :—

Constant proportionals.	Perceptible minimum.
Touch $\frac{1}{3}$	Pressure of 0·002 grm. to 0·05 grm., according to the region of the body experimented on. (Aubert.)
Muscular effort $\frac{1}{17}$ . .	Contraction of the internal rectus of the eye to the extent of 0·004 mm.
Temperature $\frac{1}{3}$ . . .	(The heat of the skin being taken at 18°·4 Cent.) $\frac{1}{8}$° Cent. (? $\frac{1}{10}$, Fechner.)
Sound $\frac{1}{3}$	Ball of cork weighing 0·001 grm. falling 0·001 m. on a plate of glass, the ear being at a distance of 91 millimeters, $3\frac{3}{4}$ inches. (Schafhäutl.)
Light $\frac{1}{100}$.	Illumination of black velvet by a candle at a distance of 8 feet 7 inches. (Volkmann.)

In seeking to find a law which shall express the general relation of excitation and of sensation, it is to be noted that we possess a knowledge of the two necessary elements—namely, the measure of the constant proportional and the measure of the smallest perceptible sensation. The first supplies the unit for dividing the standard into equal parts, the second serves to graduate it, since it determines the zero and renders it fit for use. This may be understood by reference to the following Figure :—In a line, ×, of indefinite length, a zero, 0, is noted. This answers to the minimum of sensation. Starting from the point 0, the line × is divided into equal parts, 1, 2, 3, 4, &c., which represent the increments of sensation. From the point 0, a line, 0 *b* of any length is drawn; it represents the minimum stimulus, say the 1-50th of a gramme if sensations of pressure are under consideration. Now, since the constant proportional, that is to say, the smallest perceptible difference $=\frac{1}{3}$ for pressure, a line drawn from the point 1 must equal the line 0 *b* plus $\frac{1}{3}$ of this line; from the point 2 a line equal to the line 1, plus $\frac{1}{3}$ of 1; from the point 3 a line equal to 2, plus $\frac{1}{3}$ of 2; and from the point 4 a line equal to 3, plus $\frac{1}{3}$ of 3. The third added is thus always an increasing quantity, and as the vertical lines have necessarily the same relation to one another as the weights they represent, it is clear that the differences of length between the line 0 and the lines 4, 5, 6, &c., indicate what weight must be employed in order that the perceptible difference should be quadrupled, quintupled, &c. The psycho-physical law which

Fechner has deduced from this is that within certain limits *sensation increases as the logarithms of the stimulus;* in other words, sensations increase as the logarithms, whilst the excitations increase as ordinary numbers. If we represent the stimulus as R and the corresponding sensation as S, while C represents the constant proportional, then $S = C \log. R$ when the minimum stimulus is taken = 1. This psycho-physical law only holds good within a certain limit. Beyond this the sensation increases more and more slowly, and soon a maximum excitation is reached, beyond which the relation between stimulus and sensation no longer obtains.

Fig. 282.



CHAPTER XV.

ON THE STRUCTURE AND FUNCTIONS OF MUSCULAR TISSUE.

1. *Structure of Muscular Tissue.*

613. The capability of executing movements effecting change of place or of form is a power that is so widely distributed through the animal body, that it has been questioned whether every cell or mass of germinal matter does not possess it at some period of its development. The gradual alteration of shape exhibited by the white corpuscles of the blood (§ 174), by the corpuscles of lymph (§154) and pus (§ 324), by the salivary corpuscles (§ 104), and connective tissue (§ 45), and by pigment* (§ 44) and cartilage cells as well as the rhythmical protoplasmic movements observed in the eggs of osseous fishes,† represent, perhaps, the simplest modes in which this power is displayed. The movements presented by the greater number of these cells or corpuscles resemble those performed by the germinal mass of which an Amœba is composed, the form altering from round to oval or guitar shape, and processes being thrust out at various points into which the body of the corpuscle is again drawn, by which a veritable locomotion is effected. The movements occurring in the fission and cleavage of cells appear to belong to the same category. In all these instances the motions are usually slow and interrupted, but are rendered more energetic and lively by warmth and electricity, and are retarded by cold. In Dr. Ransom's experiments, the presence of oxygen in the surrounding medium was found to be requisite for the exercise of the property of the rhythmic contractility possessed by the food yolk, as well as of the fissile contractility of the formative yolk, whilst, on the other hand, the presence of carbonic acid rapidly checked or altogether

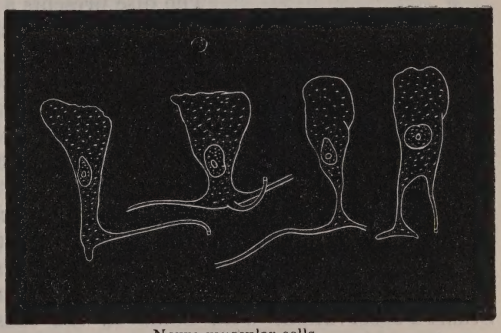
* The pigment cells in the skin of the frog appear, from the experiments of Mr. Lister, "Phil. Trans.," 1858, to be in some measure under the influence of the nervous system, and the black particles in them when set free by the rupture of the cell, exhibit remarkable quivering movements, termed Brownian movements.

† W. H. Ransom, M.D., Humphry and Turner's "Journ of Anat. and Physiol.," vol. i. p. 237.

arrested them.* The several movements here alluded to appear to be of the same kind as those observed in the contraction of muscle, only that the power is generally diffused through the whole of the cell or mass of germinal matter, instead of being limited to an organ of definite structure; just as in some of the lower animals the power of perceiving light seems to be diffused through the body, when no distinct organ of vision has as yet been developed.

614. A second kind of movement is presented by the cells of ciliated epithelium (§ 44), which line parts of the respiratory and genito-urinary apparatus in man, and in him appear to have as their office the establishment of currents directed towards the exterior of the body in the fluids covering the surface of these membranes; whilst in animals they frequently constitute important agents in effecting locomotion and in the procurement of food. The cilia of each cell do not vibrate simultaneously but successively, and the vibrations, which are upwards of 700 per minute,† do not appear to be in any way under the control of the nervous system, since they persist long after somatic death. When they have become languid they can be made to recur with vigour for a short time by the addition of a small quantity of a dilute solution of potash or acetic acid. Engelmann‡ has shown that the energy of ciliary movements rises with the temperature up to 40° C. (104° F.), but rapidly diminishes above that temperature, whilst it again increases as the temperature falls. Distilled water first accelerates, then gradually arrests, ciliary movement. The movement can be re-established by the addition of 1·5 per cent. of sodium chloride, stopped by the addition of 5 per cent., and again set in action by the addition of distilled water. The vapours of ether and chloroform first accelerate for a longer or shorter period, and then arrest the movement. Carbonic acid gas soon arrests the movements, but the admission of oxygen gas leads to their renewal,§ and this alternate action may be kept up for two or three times; when they have stopped they can also be renewed by the action of induced currents of electricity.‖ In the hydroid polypes the body is composed of two layers of cells, the outer of which is named the ectoderm and the inner the endoderm. These are separated by an intermediate fibrous layer or mesoderm, which may

Fig. 283.



Neuro-muscular cells.

* See also Rossbach, 'Die rhythm. Bewegungserschein. der einfachsten Organism. und ihr Verhalten gegen physikal. agent. und Arzneimittel,' in "Verhand. d. Phys.-Med. Gesellsch. in Würzburg," Band ii. p. 179; Abst. "Centralblatt," 1872, p. 490.

† Engelmann, "Centralblatt," 1867, No. 42.

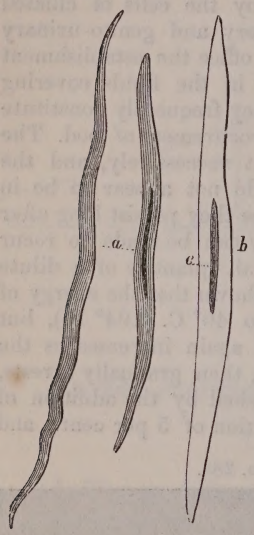
‡ 'Flimmerruhr u. Flimmermühle,' Pflüger's "Archiv," Band xv. 1877, p. 502.

§ See Kühne, Schultze's "Archiv," Band ii. 1867, p. 372, and Klein, in Sanderson's "Physiological Handbook," 1873, p. 21.

‖ Bowditch's ('The Force of Ciliary Motion,' "Centralblatt," 1877, p. 118; "Boston Med. and Surg. Journal," 1876, August 10) experiments show that the work done by the ciliated cells is equal to the raising of their own weight 4·253 metres. That of the striped muscular tissue of the heart is 35 times greater. Jeffries Wyman found that a weight of from 1–3 grammes placed on 12 square mm. of the ciliated mucous membrane of the frog was moved 15 mm. in one minute.

easily be shown to be contractile. On macerating the animal in dilute acid, the cells may be isolated, and it then appears that the contractile elements are in reality prolongations of the cells of the ectoderm. These cells therefore consist of two segments, an outer segment, containing a nucleus surrounded with granular protoplasm, and an inner segment which possesses a contractile power. Kleinenberg has applied the term '*neuro-muscular cells*' to these bodies, believing that they represent in its simplest and most rudimentary form the connection between nerve and muscle. The outer part of the cell constitutes an organ of sensation which is not yet differentiated, except in function, from the internal contractile part; and it is noticeable that even in the higher animals the central parts of the nervous system are formed from an involution of the epiblast, and that consequently there is a community of origin between the cells of the integument and those of the nervous system.* Ranvier† states that the cilia are stained yellow with picrocarminate of ammonia and blue with anilin, in these respects resembling the protoplasm of ordinary cells. Between the line of insertion of the cilia and the cell-protoplasm is a disc ('plateau') which covers the whole free surface of the cell, and is rapidly and strongly stained with aniline but not with picrocarminate of ammonia. The disc presents a series of beads, which are the swollen bases of the cilia. The cilia, therefore, perforate the disc and rest on the cell-protoplasm; but Ranvier has been unable to corroborate the assertion of Eberth and Marchi, that they may be traced to the nucleus of the cell.‡ The vibratile motions presented by the spermatozoa appear to be of the same nature as those of ciliated epithelium, and each zooid may be regarded as a cell, provided with a single cilium. Dr. A. Stuart,§ who describes the processes as extending from the base of each cilium to the nucleus and attached extremity of the cell, regards them as extremely fine muscular fibres. Dr. Stuart's observations were made on the cells of the ciliated epithelium of certain species of Eolis. He has counted from 40 to 60 bands in each cell, and describes the nucleus of the cell as being moved hither and thither by their contraction.

Fig. 284.



Fusiform cells of *Smooth Muscular Fibre*, from the renal vein of Man: *a*, two cells in their natural state, one of them showing the staff-shaped nucleus; *b*, a cell treated with acetic acid, with its nucleus *c* brought strongly into view.

615. Putting aside these cases, however, all the sensible movements of the body are effected by one or other of two forms of tissue to which the term muscular has been applied. The first of these, termed the smooth or unstriped variety of muscle, consists of flattened bands, destitute of sarcolemma, which are composed of long, fusiform cells (Fig. 284), each with an elongated oval nucleus, which become staff-shaped after death.‖ Around the nucleus is a little finely granular protoplasm, which extends for some distance in the axis of the fibre, and which can sometimes be shown to possess

* See Ranvier, "Système Musculaire," p. 44. † "Système Musculaire," 1880, p. 434.
‡ Marchi's observations were made on the Anodon, and are supported by those of Dr. A. Stuart. § "Zeits. f. rat. Med.," Band xxx. p. 288.
‖ Schwalbe, Schultze's "Archiv f. Microscop. Anat.," Band iv. p. 392, pl. xxiv.

a longitudinal striation;* the length of the cells varies from 1-1125th to 1-50th of an inch, and their breadth from 1-5625th to 1-1125th of an inch. The cells can best be isolated according to Moleschott by maceration in a solution of 35 per cent. of caustic potash.† The nerves distributed to unstriated muscle form a plexus, containing both medullated and non-medullated fibres, and present a few scattered ganglion cells. From this primary plexus a secondary plexus arises, composed of non-medullated tissue alone, with nodal swellings at the points of intersection, and the finest ramifications either run along the side of the muscle elements (Gscheidlen) or penetrate them to reach the nucleus and nucleoli (Arnold). This form of muscular tissue is found in a nearly pure state, unmixed with other tissue, in the nipple, corium, intestinal canal, bladder, prostate, vagina, and in the smaller arteries, veins, and lymphatics; and mingled with much areolar, fibrous, and elastic tissue in the trabeculæ of the spleen and corpora cavernosa, the dartos, the circular fibres of the larger arteries and veins, the urethra, Fallopian tubes and uterus, in the trachea and bronchi, and in the ciliary muscle of the eye, the choroid coat, and the iris. The principal features of the contraction of unstriated muscle may be observed in the uterus of rats and rabbits. In these organs, when exposed, and due precautions in regard to temperature and moisture are attended to, spontaneous contractions, travelling at the rate of about one inch per second, may be seen to occur at intervals of from ten to twenty seconds; mechanical stimulation applied to any point produces two waves of contraction—an ascending or antiperistaltic and a descending or peristaltic; a ligature applied to the middle of the ureter arrests the progress of the spontaneous waves of contraction to the lower segment, which remains motionless, whilst the upper part continues to exhibit the intermittent contractions; an isolated portion of the ureter remains quiescent unless stimulated, when contraction occurs. It is difficult to explain the cause of the movements, but it is probable that they are initiated by the nervous system, the contraction then being propagated from fibre to fibre.

616. The second variety of Muscular tissue presents transverse striæ under the microscope, and occurs in all those muscles that are usually termed "voluntary," though its presence in the heart, rectum, and pharynx shows that it is not limited to these alone.‡ On examining the structure of a striated muscle it is found to be easily separable into coarser or finer *fasciculi* connected by means of areolar tissue, and these on more minute dissection can be shown to consist of transversely striated polygonal *fibres* with three or five angles, having, in Man, an average diameter of 1-400th of an inch. The fibres frequently terminate by free pointed extremities in the muscle, and occasionally divide; at other times they become continuous, either abruptly or by imperceptible gradation with tendinous or strong connective tissue fibres.§ In the case of the heart, the tissue is stated by Eberth‖ and Schweigger-Seidel¶ to be composed of transversely striated oblong cells, often forked at their extremities, and containing one or several nuclei (§ 214),

* Ranvier, "La Système Musculaire," 1880, p. 382.

† Engelmann considers that the disintegration of the fibres into fusiform cells is artificial.

‡ In the Echinodermata, Vermes and Mollusca, Schwalbe ("Archiv f. Mic. Anat.," Band v. 1868, p. 205) has shown that muscular fibres exist which present double oblique striation, or two sets of oblique symmetrical decussating lines.

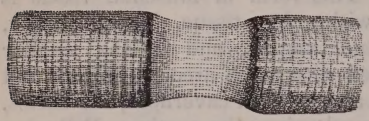
§ As in the tongue, Hyde Salter, in "Cyclop. Anat. and Phys.," vol. iv. p. 1132. Hoyer, however, maintains that in such instances the transparent fibres in which the muscular fibres apparently terminate are in reality contractile. See Reichert's "Archiv," 1859, p. 481.

‖ Virchow's "Archiv," 1866, Band xxxvii. p. 100.

¶ Stricker's "Hum. and Comp. Histology," Syd. Soc. Transl., vol. i. p. 244.

Fig. 118). The divarication of the terminal portions and the occasional presence of lateral processes, give rise to the illusory appearance, described by Skey and others, of anastomoses occurring between the fibres.* The length of the fibres in the Sartorius varies, according to Krause, from one-third of an inch to one inch and a half; whilst, according to Dr. Nicol,† in the small muscles of the hand they are co-equal with the length of the muscle, and in the muscles of the forearm vary from 1-25th of an inch to one inch. During life the fibres of striated muscle appear to be semi-transparent and of soft consistence.‡ After death each fibre can be split either longitudinally into *fibrillæ*, the number of which has been estimated at six or seven hundred, or transversely into a series of disks; the average diameter of the fibrillæ is 1–9400th of an inch in man, and they are bound together by a transparent sheath, the sarcolemma (Fig. 285) § (between which and the contractile substance a distinct layer of protoplasm sometimes exists as in the muscular fibres of the crab). Immediately beneath the sarcolemma (mammals) and sometimes in the interior of the fibre (amphibia, birds, fishes), are 'muscle corpuscles.' These consist of a nucleus with one or two nucleoli, and an investing layer of protoplasm which sends off long processes that communicate with those of other corpuscles, so as to form a delicate network of fibres beneath the sarcolemma. The corpuscles are readily brought into view by the action of acetic acid. According to some observers these are to be regarded as the remains of the original cells from which the muscular fibres were developed; others have regarded them as centres from whence new muscular fibres may originate; others, as the corpuscles of the connective tissue distributed

Fig. 285.



Muscular Fibre broken across, showing the untorn *Sarcolemma* connecting the fragments.

* It is usually stated that no sarcolemma exists around the cardiac muscular fibres. Winkler, however, describes it as being present in the form of an extremely delicate membrane. Reichert's "Archiv," 1867, p. 221.

† Schmidt's "Jahrbücher," Band cxxxii. 1866, p. 148.

‡ Kühne ("Physiol. Chemie," 1868, p. 281; also Marey, "Rev. des Cours Scient.," tome iii. p. 797) observed a Nematoid worm (Myoryctes Weissmannii), move with apparent freedom in the interior of a fibre. The movements of the worm displaced the striæ, which as it passed onward resumed their natural position. Besides this evidence of the semi-fluid nature of the contents of the fibre, it has been found that when a current of electricity is passed through a few muscular fibres, the substance of the muscle accumulates around the negative pole, indicating a certain freedom of movement in the constituent particles.

§ The following authorities may also be consulted:—Schwalbe, 'Ueber den fein. Bau d. Muskelfasern wirbelloser Thiere,' Schultze's "Archiv," Band v. p. 205; Ratzel, Histol. Unters. "Zeits. f. wiss. Zool.," Band xix. p. 257; Schneider, "Ueber die Muskeln der Nematoden," idem, p. 284; Grenacher, "Ueber die Muskelelemente von Gordius," idem, p. 287; Montgomery, 'Zur Frage über die Struct. u. Contract. quergest. Muskelfasern,' "Centralblatt," 1870, p. 163; Ranvier, 'Note sur la Structure intime du Tissue Musculaire,' in French Translation of Frey's "Histology," 1870, p. 366, and "Comptes Rendus," t. lxxvii. 1873; Merkel, 'Der quergestreifte Muskel,' Max Schultze's "Archiv," Band viii. 1872, p. 244; Dönitz, 'Beitrage zur Kenntniss der quergestreifte Muskelfasern,' Reichert's "Archiv," 1871, p. 434; Wagener, 'Ueber die Querstreifen den Muskeln,' "Sitzungsber. d. Gesell. zur Marburg," 1872, pp. 25, 117, 141; Grunmach, 'Struktur der Muskelfasern bei den Insekten,' "Centralblatt," 1872; Engelmann, 'Mic. Untersuch. ü. d. quergestreifte Muskelsubstanz,' Pflüger's "Archiv," Band vii. pp. 33 and 155; Sachs, 'Die querstreifte Muskelfasern,' Reichert's "Archiv," 1872, p. 607; Krause, "Göttingen Nachrichten," Aug. 1868, p. 357, "Zeits. f. Biologie," Band v. 1869, p. 414; and Pflüger's "Archiv," 1873, Band vii. p. 508; Floegel, Schultze's "Archiv," Band viii. 1871, p. 69, and "Med.-Chir. Rev.," 1872, p. 520; Hénocque, "Lancet," 1870, vol. i. p. 812; Hensen, "Arbeiten aus dem Kiel Physiolog. Institut.," 1868; Dwight, "Month. Mic. Jour.," vol. xii. p. 29; Thin, "Q. J. Mic. Sci." vol. xvi. 1876, p. 251.

through the muscle, and therefore as centres of nutrition analogous to the lacunæ of bone; and still more recently it has been maintained that they are in connection with the ultimate terminations of nerves. The exact structure of the fibrillæ is still doubtful. Under high powers of the microscope they appear to consist of alternate rectangular light and dark bands, constituting the "sarcous elements" of Mr. Bowman. The dark bands are thicker than the light ones, and in consequence of their being less easily acted on by dilute hydrochloric acid and gastric juice, can be obtained in a detached or separate state after short exposure to the action of either of these fluids. Brücke has described the dark particles as refracting light doubly (anisotropous), whilst the clear intervening substance is only singly refractile (isotropous).* He regards the dark particles as uniaxial positive crystals, having their axes parallel to the direction of the fibres, and as being composed of minute solid doubly-refracting particles, which he terms *disdiaclasts*. Engelmann† describes each fibre as being, when fresh, almost perfectly transparent and homogeneous, but speedily undergoing a kind of coagulation, which is hastened by the addition of any reagent, and results in the appearance of a series of superimposed disks, varying in their thickness and their action on light. These confer upon the tissue its peculiar striated aspect, and the adjoining Figure (286) exhibits them in a diagramatic form. The column formed by each fibril is, in the first place, divided at regular intervals by septa, *z*, which, as they are at the same level in adjoining fibrils, run across the whole fibre. The septa divide the fibrils into compartments named by Engelmann 'muscle elements,' and by Krause 'muscle caskets,'§ and the contents of each casket are laminated. The *septal* or *intermediate disks* are composed of a homogeneous membrane, which with sharp focussing forms the darkest stria of the fibre; water and various reagents make it granular or beady, though the

Fig. 286.

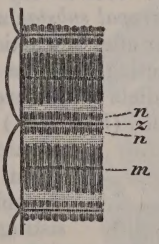


Fig. 287.

Structure of striated muscular fibre after Engelmann.‡ Fig. 286, from *Telephorus melanurus*. Cutaneous muscle from the abdomen. *m*, median disk; *n*, secondary disk; *z*, intermediate disk, magnified 1000 diam. The sarcolemma is seen on the left side. Fig. 287, from *Astacus fluviatilis*. Heat tetanus. *n*, secondary disk; *z*, intermediate disk; *i*, isotropous disk between transverse and secondary disk; *i*, isotropous disk between secondary and intermediate disk; *m*, median disk; *q*, *q*, transverse disk. The sarcous elements are swollen at their extremities, and at their centres. Magnified 1000 diam.

* See Stricker's "Hum. and Comp. Histology," Syd. Soc. Trans., vol. i. p. 235, 1870. Dr. Martyn (Beale's "Archiv," 1862, p. 227), in examining a fortunate specimen of muscular tissue under a very high power (1,200 linear), observed large and small sarcous elements to occur alternately, as had previously been described by Busk and Huxley (Note to Kölliker's "Man. of Hum. Histology," Syd. Soc. Trans., vol. i. p. 239); the smaller one evidently corresponding to the faint transverse line traversing the clear space long ago perceived and described by Dr. Sharpey and the Author, from careful observation of Mr. Lealand's preparations. Dr. Macnamara ("Med. Times and Gazette") describes the muscular *fibres* of the chameleon when examined with the highest powers ($\frac{1}{50}$) as composed of a sheath of sarcolemma containing two longitudinal flat bands, connected by a spirally wound band, the shadow or the approximation of two coils of which forms the transverse striæ. Between the horizontal bands are *open spaces*, as is shown by their never becoming stained with carmine. M. Rouget (Brown-Séquard's "Journ. de la Physiologie," and "Med.-Chir. Rev.;" see also "Comptes Rendus," 1867, pp. 1128, 1232, and 1276) regards the elementary *fibrilla* of striated muscles as being a spirally twisted ribbon, of which the coils, ordinarily separated from one another or stretched, approximate on the removal of all exciting and nutritive conditions.

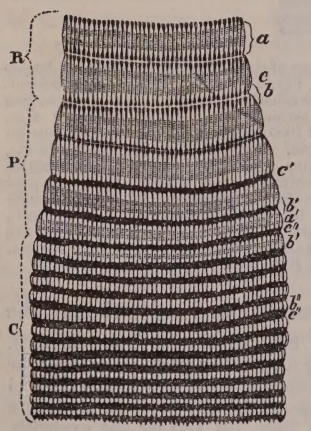
† Engelmann, Pflüger's "Archiv," Band vii. pp. 33–71; see also Schäfer, "Philosoph. Transact.," 1873, p. 429.

‡ Pflüger's "Archiv," Band vii. p. 70. For another view of the structure of striated muscular tissue, see Heppner, Schultze's "Archiv f. Mik. Anat.," Band v. p. 137.

§ Muskel-kästchen.

fibre may still retain its contractile power. It is doubly refracting, and its greatest thickness (in Articulata) is 0·0008 mm. It is highly elastic—*i.e.*, is compressed and extended with difficulty. The sarcolemma presents either an annular groove, or an elevation where it is attached to it, and the connection between the two is usually firm. 2. The *isotropal layer* between the septum and the collateral or secondary disk is almost immeasurably thin. 3. The *secondary* or *collateral disk* (*n*), Flögel's 'granule layer,' has a thickness of 0·002 mm. This is usually separated from the anisotropal substance by a thin layer of isotropal substance, but is sometimes fused with it, as can easily be determined by polarized light, the anisotropal substance then appearing much thinner, since the collateral disk presents but feeble indications of double refraction. It adheres less firmly to the sarcolemma than to the septal disk. In breaking a fibre across mechanically, the rupture commonly occurs between the collateral and the transverse disks. In mammals the septal or intermediate and the collateral disks appear to be fused together. 4. The *isotropal layer* between the secondary and transverse disks in Vertebrata has a thickness of 0·001 mm., and in Arthropods of 0·0015. This is very soft, but still not fluid, as Kühne thought. 5. The *layer of anisotropal substance* consisting of two transverse and a median disk (*m*). This layer after the action of many reagents appears to be formed of solid doubly-refracting rod-like elements, the so-called sarcous elements, muscle prisms or rodlets which are imbedded in a softer, singly-refracting amorphous substance. (Fig. 287.) The rods, according to Engelmann, are certainly not preformed elements. The account given by Schäfer differs considerably from the foregoing. He describes a muscular fibre as consisting of a ground substance, appearing at first sight to be composed of a series of alternately dim and bright disks, and of a vast number of minute rod-like particles, to which he applies the term muscle-rods, which are closely arranged side by side with their long axes parallel to the axis of the fibre, so as to form by their juxtaposition as many series as there are disks of dim substance in the fibre. The main part or shaft of each muscle-rod is imbedded in and traverses a disk of dim substance, while the ends which are enlarged into little knobs or heads extend into the bright disks. These little knobs form the line of dots which has long been described as existing in the middle of each bright stripe. When the fibre is somewhat extended this line appears double, owing to the separation of the heads of the two successive series of muscle-rods which meet in the middle of the bright substance. In the state of absolute rest (R, Fig. 288) the rods are uniformly cylindrical without terminal enlargements, and in this case only a longitudinal fibrillation is to be seen in the fibre, all trace of transverse striping having disappeared. In the normal state of slight tension however (P), the rod-heads make their appearance, and with

Fig. 288.



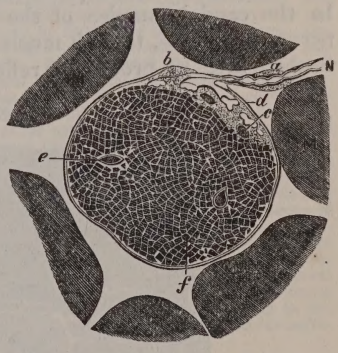
Muscular fibre undergoing contraction. R, portions still at rest; P, contraction proceeding; C, contracted portion; *a a'*, dim stripes; *b b' b''*, bright stripes; *c c' c''*, lines formed by rod-heads.

Fig. 289.

Diagram representative of Mr. Schäfer's view of the structure of muscular fibre.
1. Dim substance.
2. Bright stripe.
3. Muscle rods.

them the bright substance by which they are surrounded, so that the dim ground substance now presents a transversely striated aspect. In contraction of the muscle the heads of the rods become enlarged at the expense of the shaft, the ends of the several muscle-rods thus approaching one another, and forming, with the heads of the next series of muscle-rods, a dark transverse band crossing the bright stripe. As the contraction proceeds, the dark bands approximate to one another, the bright borders encroach upon the dim stripe, which finally disappears, so that its place is taken by a single transverse bright stripe (c). Contracted muscle consequently shows alternate dark and bright stripes, the former, however, being due to the enlarged juxtaposed extremities of the rods, the light on the other hand being mainly composed of the ground substance which has become accumulated in the intervals between their shafts.* Examined by polarized light, the muscle-rods give indications of being isotropous or singly refracting, whilst the remainder of the fibre is anisotropous. The latter is probably the true contractile part, whilst the rods are merely elastic structures, serving to restore the fibre to its original length. The muscles receive a free supply of blood, especially during action,† the capillary vessels being arranged in oblong meshes ; but their lymphatics are either altogether absent or exceedingly few in number.‡ The mode of termination of the nerves in muscle has recently been the subject of much investigation.§ According to Kühne and Engelmann, the motor nerves divide and subdivide till the fibres run alone or only in bundles of two or three on the outside of the muscular fibres. After a short course, however, they penetrate the sarcolemma, losing at the same time their sheath, which becomes continuous with the sarcolemma, and the white substance of Schwann; whilst the axis-cylinder, dipping in amongst the fibrillæ, terminates in a nerve-plate or disk, which melts by imperceptible gradations into the tissue of the muscle itself. Cohnheim,‖ whilst agreeing with Kühne in admitting the penetration of the sarcolemma by the nerve-fibres, represents these as branching and dividing to a considerable extent. Kölliker, Beale, and Krause,¶ on the

FIG. 290.



Transverse section of one of the muscles of the thigh of *Lacerta Agilis*, made whilst frozen, and magnified 400 diameters. N, nerve. M, muscular fibre, surrounded by portions of six others. *a*, Nucleus of the nerve sheath; *b*, nucleus of the sarcolemma; *c*, section of nucleus of terminal plate of nerve; *d*, transverse section of terminal plate, surrounded by granular material; *e*, transverse section of muscle nuclei; *f*, fine fat drops. The angular dark particles are sections of groups of sarcous elements and form Cohnheim's areas; the clear intervening spaces represent the fluid isotropal part of the muscle substance.

* Mr. David Newman ("Journ. of Anat. and Physiol.," vol. xiii. 1879, p. 549) has recently suggested a new theory of contraction of striated muscle, in which he conceives that Krause's compartments contain a plasma, which during a state of rest holds the whole of its combined fat in complete solution, and is doubly refracting, but in the act of contracting the plasma precipitates its fat, which collects in the form of a flattened disk at the centre of the cylinder. The plasma, thus freed from its fat, forms the light band, and is only singly refracting.

† Sczelkow, "Centralblatt," 1870, p. 691.

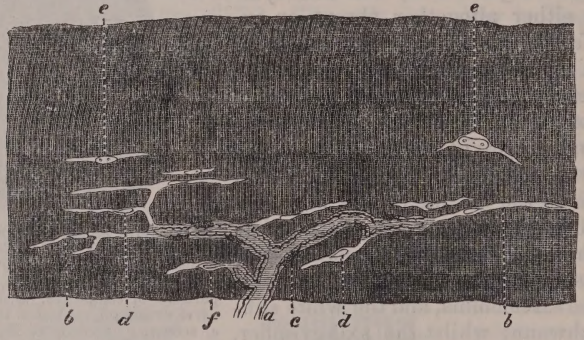
‡ Teichmann, "Das Saugader System," 1861, p. 100.

§ See Kühne, "Ueber die peripheric. Endorgane der motor Nerven," 1862; Engelmann, T. W., "Untersuch. üb. d. Zusammenhang v. Nerv- u. Muskel-faser," Leipzig, 1863; Kölliker, Croonian Lecture, 1852; Beale, "Archives of Medicine," vol. iii. 1862, p. 246; "Philosophical Transactions," 1863; Croonian Lecture, 1865; and "Distribution of Nerves to Voluntary Muscles: an Anatomical Controversy." Pamphlet, Churchill, 1865.

‖ Virchow's "Archiv," 1865, pp. 194 and 606. ¶ "Zeits. f. rat. Med.," Band xxxiii. and xxxiv.

other hand, deny the penetration of the sarcolemma by the ultimate branches of the motor nerves, the two former observers describing them as forming a plexus, composed of pale fibres of extraordinary tenuity (1-100,000th of an inch), intermingled with many nuclei lying on and ramifying *over* the fibres. Mayo describes a similar plexus within the sarcolemma, whilst Krause admits the plate, but believes it to be outside the sarcolemma. The three accompanying drawings, Figs. 290–292, will render the views of Kühne, Cohnheim, and Beale intelligible. The proportion of nerve-fibres in the motor nerve trunks to the number of the muscular fibres, in the muscles to which they are distributed, varies considerably.* Tergast finds in the ocular muscles of the Sheep that there is one nerve-fibre to about 6 or 7 muscular fibres. In the ocular muscles of Man there are about 3 nerves to 7 muscular fibres. In the biceps of a young Dog there is one nerve-fibre to 83 muscular fibres; in the sartorius of the same animal 1 to 40-60. In the cutaneous pectoral of the Frog the proportion is 1 : 23–27 (Reichert); in the abductor digiti quinti pedis 1 : 40; in the sartorius 1 : $16\frac{1}{2}$; in the ocular muscles of the same animal, 1 : 10. In the caudal muscles of the Mouse, 1 : 28-29. The presence of sensory nerves in muscle, though much disputed, seems to have been demonstrated by Sachs,† first, by producing reflex convulsions on irritation of the central end

FIG. 291. (After Cohnheim.)



Muscular Fibre, with termination of Motor nerve, from the Gastrocnemius of *Rana esculenta*: —*a*, Terminal pencil of a dark-bordered nerve-fibre; *b*, Intra-muscular naked axis cylinder; *c*, Nucleus of the neurilemma; *d*, Clavate extremities of the nerve; *e*, Muscle-nuclei; *f*, Terminal knob of nerve, with central fibre and vesicular dilatation of the nerve.

of the nerve entering the sartorius in a frog poisoned with strychnia, such convulsions occurring even when the anterior roots of the spinal nerve had been divided; secondly, by showing that after section of the anterior roots of the sciatic plexus, though degeneration of the greater part of the nerve supplying the sartorius occurred, yet that two doubly-contoured fibres remained undegenerated; and, thirdly, by showing that the mode of distribution of the motor and sensory nerve fibres differs, the former dividing dichotomously, and the latter in an arborescent manner.

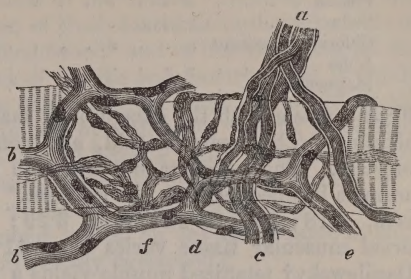
617. *Chemical Composition of Muscle.*—The muscles of cold-blooded animals are well adapted for chemical investigation on account of the slowness with which they undergo change. If the muscles of such an animal, after the removal of all blood from the tissue by the injection of a very weak solution of common salt, be subjected to pressure, a neutral or weakly alkaline fluid is

* See Tergast, Schultze's "Archiv f. Microscop. Anatomie," Band ix. p. 36.
† "Archiv f. Anat. u. Physiol.," 1874.

obtained, termed "muscle-plasma," which soon undergoes spontaneous coagulation, and separates into two parts—a semi-solid portion termed myosin (§ 55), and a fluid serum, which at ordinary temperatures quickly acquires an acid reaction. In the latter, as obtained from various animals by different chemists, there have been discovered: 1. Various albuminous compounds, and compounds nearly allied to albumin. 2. Ferments, as pepsin (Brücke); and a substance analogous to, if not identical with, ptyalin (Piotrowski), or amylopsin, and a lactic acid producing ferment. 3. A colouring matter similar to, if not identical with, hæmoglobin.* 4. Kreatin (§ 56), and perhaps kreatinin,† hypoxanthin or sarkin, carnin, xanthin, and taurin. 5. Urea, inosinic and uric acids. 6. Sugar, inosit, glycogen, and dextrin. 7. An insomeric modification of lactic acid, termed para- or sarco-lactic acid, acetic, formic, and butyric acids. 8. Salts, which, as obtained from the residue of broth, consist in 100 parts‡ of

PO_5	26·27
Cl	1·63
K	9·40
KO	40·10
SO_3	3·59
$2\ CaO,PO_5$	3·06
$2\ MgO,PO_5$	5·76
$2\ Fe_2O_3,PO_5$	0·57

Fig. 292. (After Beale.)



Portion of an Elementary Muscular Fibre from one of the abdominal muscles of the *White Mouse*, with four dark-bordered fibres (*a*) crossing over its surface. A capillary vessel, *b*, is also seen with fine nerve-fibres distributed to it. To avoid confusion, a few only of the transverse markings of the muscle are represented. Two of the dark-bordered nerve-fibres (*c*), pass over the elementary fibre, to be distributed to adjacent fibres. One dark-bordered fibre (over *d*) is lost among several pale nucleated fibres. Pale nucleated fibres are seen ramifying in several places upon the surface of the elementary fibre, but beneath the dark-bordered nerve-fibres and capillaries. It will be observed that a fine fibre, which seems at the upper part of the figure to be but one of the outlines of the tubular membrane of one of the dark-bordered fibres, leaves the dark-bordered fibre and passes to the capillary vessel (over *e*). This arrangement, in which a dark-bordered nerve-fibre distributed to a muscle divides into branches, one of which passes to a vessel, while the other ramifies upon a muscle, is frequent. The capillaries, dark-bordered nerve-fibres, and pale nucleated fibres here represented, can be completely stripped off from the surface of the sarcolemma without tearing that membrane. Of the structures, therefore, represented in this drawing, not one, according to Dr. Beale, after whom it is taken, can lie beneath the sarcolemma. (× 700.)

9. A small proportion of fat. 10. Water, carbonic acid, and oxygen gases; and, lastly, various compounds derived from the tissues which are inseparably united with the muscular tissue, as protagon, proceeding from the nervous, gelatin from the connective, and elastin from the vascular tissue. The composition of muscle as a whole is thus given by Kühne, after Lehmann:—

Water	74·0—80·0
Solid constituents	26·0—20·0
Albuminous substances insoluble in water (myosin, sarcolemma, nuclei, vessels, and elastic fibres)	15·4 —17·7
Gelatin	0·6 — 1·9
Albuminates of soda, coagulating at 113° F.	2·2 — 3·0
Kreatin	0·07— 0·14
Fat	1·5 — 2·30
Lactic acid	1·5 — 2·30

* Lankester, Pflüger's "Archiv," Band iv. p. 315.

† Nawrocki, Fresenius' "Zeits. f. Analyt. Chemie," 1865, p. 330, denies the presence of the latter, or that any conversion of kreatin into kreatinin occurs during exercise.

‡ Kühne, "Physiol. Chemie," 1868, p. 307, in which work a very complete account of the chemistry of muscle is contained.

Phosphoric acid	0·66—0·70
Potash	0·50—0·54
Soda	0·07—0·09
Chloride of sodium	0·04—0·09
Lime	0·02—0·03
Magnesia	0·04—0·05

Fresh muscle, with the exception of that of the heart, is either neutral or faintly alkaline. The heart is acid, and contains a little more water than other muscles. The percentage proportion of nitrogen in the flesh of different animals has been shown by Petersen* to vary: thus mutton contains 3·15; veal, 3·18; pork, 3·25; beef, 3·29; and horseflesh, 3·48. Its amount in dried muscular tissue varies from 11·88 to 15·07 per cent. According to Danilewsky† tetanized muscle yields a little more nitrogen to warm alcohol, which dissolves the products of its disintegration, than muscle at rest. Amongst these is lecithin. Muscular tissue, whether living or dead, absorbs oxygen, and eliminates carbonic acid,‡ though more energetically in the former case than in the latter. The specific heat of muscle exceeds that of water, and is higher than that of any known solid or fluid body.§ It is, on the other hand, an exceedingly bad conductor of heat. Glycogen is a constant constituent of muscle, the quantity varying from about one-half to one per cent. It augments when the muscles are kept at rest,‖ and diminishes with exercise, and especially after tetanus. In Rabbits the muscles of the back contain nearly a fourth more than the adductors of the thighs. It diminishes considerably after fasting, but rapidly increases above the normal when much starchy food is taken.¶ It is increased after division of the motor nerves supplying the muscle,** but is diminished after ligature of the arteries.††

618. *Development of Muscular Tissue.*—In Man, according to Mr. Lockhart Clarke,‡‡ Muscular Fibre can first be distinguished about the fourth or fifth week of utero-gestation. In a fœtus of three-fourths of an inch in length, it forms a gelatinous mass consisting of fibres and nuclei imbedded in a semi-fluid granular blastema. In the formation of the fibres, granular processes of condensed blastema extend from the sides or from around the nuclei, which are subsequently bounded by an investing substance in the form of a band or fibre, sometimes plain, but sometimes longitudinally fibrillated. In these bands the transverse striation first makes its appearance, and only subsequently extends through the central band or axis. The muscular fibres vary in size at different parts, and they may sometimes be seen to increase in diameter by the adhesion of fresh nuclei and fresh processes of blastema. A very similar account has been given by Mr. Savory for the Mammalia generally,§§ except that in his observations the nuclei, at first irregularly distributed, were found to arrange themselves with great regularity in single rows, almost in contact with one another, the fibres being formed by the development of two nearly transparent bands enclosing and bounding the rows of nuclei; subsequently the nuclei began to separate from one another, and

* "Zeits. f. Biologie," Band vii. Heft 2.

† "Centralblatt," 1872, p. 433.

‡ Du Bois-Reymond; G. Liebig; Hermann. See the "Grundriss der Physiol." of the latter author, 1867, p. 212; R. Gscheidlen, Pflüger's "Archiv," Band viii. p 506.

§ Adamkiewicz, "Centralblatt," 1874, No. 22.

‖ Ogle, "St. Geo. Hosp. Rep.," vol. iii. p. 149.

¶ Luchsinger, Pflüger's "Archiv," Band xviii. 1878, p. 472.

** McDonnell, "Journ. of Anat. and Physiology," vol. ii. p. 275.

†† Chandelon, Pflüger's "Archiv," Band xiii. p. 626.

‡‡ "Proceedings of the Royal Society," vol. xi. No. 48.

§§ See Part ii. of the "Phil. Trans." for 1855. See also Petrowsky, "Centralblatt," 1873, p. 769.

ultimately broke up into granules and disappeared. The striation began within the border and gradually extended to the centre. Increase in the size of the fibres was effected by the addition of fresh blastema to the outer side of existing fibres. The observations of Braidwood* and of Eckhard† are, on the whole, confirmatory of the observations of Clarke and Savory; and it would hence appear that the essential features of the process occur not in the nuclei, nor in cells, as was originally maintained by Schwann, but in a material which may be regarded as intercellular substance; and Lockhart Clarke regards even involuntary muscular fibres as by no means the *product* of a nucleated cell, but rather as a kind of cell-formation, presenting at first a nucleus encrusted with blastema, around which an investing sarcous substance representing the cell-wall is subsequently developed.‡

619. The frequently renewed exercise of muscles, by producing a determination of blood towards them, occasions an increase in the nutrition; so that a large amount of new tissue is developed, and the muscles augment in size and vigour. This is true not only of the whole muscular system when equally exercised, but also of any particular set of muscles which is more used than another. Of the former we have an example in those who practice a system of gymnastics adapted to call the various muscles alike into play; and of the latter in the limbs of individuals who follow any calling that habitually requires the exertion of either pair, to the partial exclusion of the other, as the arms of the smith, or the legs of the opera-dancer. But this increased nutrition cannot take place unless an adequate supply of food be afforded; and if the amount of nutritive material be insufficient, the result will be a progressive diminution in the size and power of the muscles, which will manifest itself the more rapidly as the amount of exertion, and consequently the degree of *waste*, is greater. Nor can it be effected if the exercise be incessant, for it is during the intervals of repose that the reparation of the muscular tissue occurs; and the Muscular system, like the Nervous, may be worn out by incessant use. The more violent the action, the longer will be the period of subsequent repose required for the reparation of the tissue; and the longest time will of course be requisite when (as sometimes occurs) the contractility of the muscle is so completely exhausted by excessive stimulation that no new manifestation of it can be excited. It does not appear improbable that there is a provision in *some* Muscles, as the Heart and Respiratory Muscles, by which the nutrition is carried on with unusual activity during the short period of repose which intervenes between two successive contractions. Moreover, the muscular tissue, like all the softer and more decomposable portions of the organized fabric, has a limited term of existence; and hence, even if its contractility be not called into exercise, it undergoes a gradual disintegration so soon as all the nutritive changes of its fibres are completed. This change seems to be a necessary consequence of the high temperature of the bodies of warm-blooded animals; for it does not occur with nearly the same rapidity in cold-blooded animals, nor in the hybernating condition of certain warm-blooded Mammalia; indeed, when the temperature of the body is reduced to within a few degrees of the freezing point, no chemical change seems possible in muscle—its spontaneous decay and its vital activity being alike checked. Now, when a muscle or set of muscles in a warm-blooded animal is reduced to a state of prolonged

* "Med.-Chir. Rev.," 1866, p. 447. † "Zeitsch. f. rat. Med.," Band xxix. p. 55.

‡ Dr. Wilson Fox ("Phil. Trans.," 1865–6) has, however, resuscitated the older view of Lebert, Kölliker, and others, that the fibres of muscle proceed from the cells of the embryo, the contents of which become fibrillated, whilst the cell-wall becomes the sarcolemma.

inactivity, from whatever cause, its supply of blood is diminished, and its spontaneous decay is not compensated by an equally active renewal; so that in time the characters of the structure are changed, and its distinguishing properties are no longer presented. Thus it was found by Dr. John Reid* that in a rabbit, a portion of whose sciatic nerve had been removed on one side, the muscles of that leg were but very feebly excited to contraction by galvanism after the lapse of seven weeks. The change in their nutrition was evident to the eye, and was made equally apparent by the balance. The muscles of the paralyzed limb were much paler, smaller, and softer than the corresponding muscles of the opposite leg, and they scarcely weighed more than half—being only 170 grains, whilst the others were 327 grains. It was found also that a perceptible difference existed in the size of the bones of the leg, even after so short an interval had elapsed; the tibia and fibula of the paralyzed limb weighing only 81 grains, whilst those of the sound limb weighed 89 grains. On examining the muscular fibres with the microscope, it was found that those of the paralyzed leg were considerably smaller than those of the sound limb, presenting a somewhat shrivelled appearance, and that the longitudinal and transverse striæ were much less distinct. So in persons whose lower extremities have been long disused, the muscles first become pale and flabby; their bulk gradually diminishes; their contractile force progressively decreases, and at last departs almost entirely; and their proper structure is replaced by a deposit of fat, in which few or no striated muscular fibres can be detected. But muscles that have for some time remained in this condition may be gradually brought back to their original state by exercise, provided that the feeblest contractility remains; for every action which they can be made to perform determines an augmented flow of blood through the tissue, and gives rise to an improvement in its nutrition, which in its turn increases its contractility, and renders it capable of more vigorous action. This principle is of great importance in the treatment of the various forms of paralysis (especially the hysterical), in which the muscles are thrown out of use by the suspension of the functional power of the nerves; for when the latter have recovered their capacity, the muscles refuse obedience to their stimulation, and can only be brought to act by persevering and judiciously contrived exercise.

620. Muscles exist in two states, the elongated and the contracted; the former is usually termed their state of *rest*, in which they immediately respond to the application of stimuli, whether direct or indirect, by passing into the active state of contraction.† The physical, chemical, and electrical properties of muscles differ considerably in these two states.—In *contraction* the muscles become shorter and thicker, and diminish slightly in volume.‡ Their elasticity

* "Edinb. Monthly Journ. of Med. Science," May, 1841; and "Physiological, Anatomical, and Pathological Researches," p. 10.

† Dr. Radcliffe (see his "Epileptic and other Convulsive Diseases of the Nervous System," 3rd edit. 1860, and his "Lectures on Epilepsy, Pain, and Paralysis," 1864) has, however, adduced many arguments to show that the ordinarily received statement above given should be reversed, and that the state of elongation should be regarded as the really active condition of muscular fibre, in which all its vital properties and peculiarities are most strongly marked; whilst the state of contraction is due to its being left to the influence of the attractive forces inherent in its molecules, the most energetic operation of which is seen in the rigor mortis. According to Lavdovsky ("Centralblatt," 1871, p. 769) the unstriated muscle fibres of Leeches and Worms, when stimulated, first elongate and become attenuated, and then contract and become thickened. The number of successive contractions that can be made to occur per minute in isolated muscle-cells varies from 10–20, which is the ordinary number, to 36–40, which only happens in very lively animals.

‡ Harless, "Abhand. Münch. Akad.," 1862, p. 357. Luigi Fasci, Virchow's "Jahresbericht," 1867, p. 80.

and electrical relations are modified, and heat* and sound are produced. They absorb more oxygen. They give off, as already stated, more carbonic acid. Their reaction changes from neutral or feebly alkaline to acid, which, according to Ranke,† is due to the development of lactic acid. They contain more kreatin, grape sugar, and fat, and less glycogen.‡ From the experiments of Helmholtz,§ which have been corroborated by Ranke, it appears that the muscles of frogs long subjected to the action of an interrupted current of electricity yield from 20 to 24 per cent. less of extractives soluble in water, whilst those soluble in alcohol increase to a corresponding amount; the muscles also respond differently to electrical shocks. In tetanus, the muscles of the extremities, if the blood-current through them be preserved, become more watery (Ranke). This is particularly the case with the heart. The quantity of albumin diminishes, though only to an inconsiderable extent (Helmholtz, Ranke, Nawrocki). The heart in the case of the Dog, in comparison with the muscles of the extremities, contains much less albumin. The heart yields much more warm alcohol and less watery extract than the quiescent, and even than the tetanized muscles of the extremities. The alcoholic extract of tetanized muscle, and especially of the heart, contains more nitrogen than that of quiescent muscle.‖ It is remarkable that highly oxygenated blood, such as is the condition of the blood in apnœa, renders both the nerves and muscles unexcitable.¶

621. Numerous experimenters** have shown that the contraction of muscular tissue is accompanied by the production of a considerable amount of *heat*. Helmholtz found that on tetanizing the muscles of the thigh of a frog by stimulating the spinal cord for two or three minutes, the temperature, as indicated by a thermo-electric apparatus, rose 0·14°–0·18° C. Heidenhain found that each contraction of the gastrocnemius of a frog raised the temperature 0·001°–0·005° C. In warm-blooded animals the heat generated is much greater. Billroth and Fick†† observed a rise of 0°·5 C. or more when tetanus was maintained for ten minutes. The degree of heat developed is dependent upon the tension of the muscle, upon the amount of work done, and upon the condition of freshness or exhaustion of the muscle. With the increase of tension the amount of heat generated is augmented, so that a muscle contracted to the utmost, supposing its excitability and the stimulus to remain the same, develops the maximum of heat; hence the whole amount of heat generated increases with the amount of work done, though a portion

* In rigor mortis (Fick, in "Vierteljahrsch. der Naturf. Gesell. in Zurich," 1867), with Dybkowsky, observed a rise of 0°·05—0°·07 C., and they attribute the rise in temperature sometimes observed in bodies after death to this source, the muscles then becoming rapidly stiff.

† Reichert and Du Bois-Reymond's "Archiv," 1863, p. 422. See also his work on "Tetanus," Leipzig, 1865.

‡ "Weiss, Wien. Akad. Sitz-ber.," Band lxvi. p. 284. § Müller's "Archiv," 1845.

‖ See Danilewsky, "Centralblatt," 1872, p. 433; and Grützner, 'Ueber einige Chem. React. des thät. u. unthät. Muskels.,' Pflüger's "Archiv," Band vii. p. 254, who shows that quiescent muscle is capable of oxidizing pyrogallic acid, whilst tetanized muscle is incapable.

¶ See v. Bezold and Blöbaum, in the "Wurzburg. Physiol. Untersuch.," Heft 1, p. 66 and Mayer and Basch, "Sitz. d. kais. Acad. d. Wiss. zu Wien," 1870, p. 837. For the phenomena of exhaustion in muscle, see Volkmann, in Pflüger's "Archiv," Band iii. p. 372.

** Helmholtz, Müller's "Archiv," 1848, p. 144; Solger, "Studien des Physiolog. Instituts. zu Breslau," 1863, p. 125; Meyerstein and Thiry, "Zeits. für rat. Med.," Band xx. 1863, p. 45; Heidenhain, "Essay on the Theory of Muscular Force," Breslau, 1864, and "Mechanische Leistung, Wärme-entwicklung und Stoffumsatz," 1864; Dybkowsky and Fick, "Vierteljahrschrift der Naturforsch. Gesell. in Zurich," 1867; Schiffer, Pflüger's "Archiv f. Physiol.," 1868; and Müller's "Archiv," 1868, p. 442.

†† Wundt, "Physiologie," 1873, p. 536.

is derived from the contraction of the muscle itself. The temperature falls rapidly with increasing exhaustion, and the amount generated is inappreciable to our present means of research before the muscle has quite lost its power of contraction. The gradual increase in temperature, observed when a muscle is tetanized, continues for some time after contraction has ceased; and proceeds, in all probability, partly from the continuance of a more energetic process of oxidation, indicated by the increased production of carbonic acid, and partly from an increased flow of blood through the vessels of the muscle. According to Meyerstein and Thiry, the amount of heat generated is always in proportion to the amount of work done; whilst Heidenhain maintains that the relation between the two is inverse after a certain point has been reached. He notices also that less heat is developed if the muscle be allowed to shorten, and thus to perform work, than if it be prevented from shortening, and this may reasonably be explained on the supposition that during the active alternate contraction and elongation of the fibres the circulation through the vessels is more rapid, so that the heat locally produced is carried off by the blood. Fick* finds that the greatest quantity of heat which 1 gramme of muscle develops in a single contraction is 3·1 mcal.,† which would correspond to the combustion of 0·8 mg. of carbo-hydrate or 0·3 mg. of fat. The mechanical work performed by the muscle corresponds to only a very small part of the heat produced, varying from 1 : 3·5 to 1 : 23·6.—The peculiar *sound* heard during the contraction of striated muscle may be perceived, as suggested by Dr. Wollaston,‡ by placing the tip of the little finger in the ear, and contracting the muscles of the ball of the thumb, or by powerfully exerting the muscles which close the jaw. It resembles the distant rumbling of carriage wheels, or an exceedingly rapid and faint tremulous vibration, which, when well marked, has an almost metallic tone. From various experiments made upon himself and others, Professor Haughton estimates that the number of vibrations varies from 32 and 36 per second. The sound may be readily conceived to depend upon the friction of the elements of the muscle, one upon another, which must thus be perpetually taking place so long as it continues in a state of activity, an explanation that receives support from the observation of Helmholtz, that the pitch of the note may be made to vary by exciting contraction in the muscle with an interrupted current, the shocks of which succeed one another with varying rapidity.—The *amount of shortening* which a muscle will undergo bears a direct relation to the resistance; and by opposing a sufficient resistance, the contractile power of the muscle may be powerfully exerted without any contraction taking place. Under ordinary circumstances the striated muscles do not contract much more than one-third of their length, being restrained by the mechanical arrangements of the bones and joints, and by the antagonistic muscles. But if a long muscle of a frog be removed from the body and powerfully stimulated, it will contract to one-fifth of its original length. The unstriped fibres will contract under favourable circumstances to about one-third of their length.

622. Muscles, whether in the contracted or elongated state, possess a certain amount of *elasticity*. By this term is meant that force by which the particles of any substance, after being approximated to or separated from one another, strive to regain their original position. The elasticity of muscular fibre is small, but remarkably perfect;§ for although it is extended considerably by

* Pflüger's "Archiv," Band xvi. 1878, p. 89.

† Microcalory. The amount of heat required to raise one milligramme of water 1°C.

‡ "Philosoph. Trans.," 1811.

§ The determination of the elasticity of the muscles is attended with some difficulty, since, when stretched by a weight, they yield quickly to a certain degree, and then move slowly to

a light weight, it recovers itself completely on the removal of the extending force.* Like that of India-rubber, it is augmented by heat.† That it is exceedingly small, even during life, is shown, as Mansvelt has observed,‡ by the fact, that in cases of paralysis of the third nerve the pupil is for some days brought quite into the middle of the space between the eyelids solely through the *elastic* contraction of the rectus internus; a proof that its antagonist, in a state of elongation, exercises no force worth speaking of. On appending a small weight to a vertically-suspended fresh muscle, it at first elongates suddenly and considerably (the primary extension), then much more slowly (the secondary extension). On removing the weight, the same phenomena appear in inverse order; a considerable primary, and a more gradual and smaller secondary retraction. With small weights the increase in length is proportional to the weight; with heavier weights a greater proportional weight is required to produce the same amount of extension, as is shown in the following experiment made by Weber§ with the Hyoglossus of a Frog:—

Weight in Grammes successively applied to the Muscle.	Length of the Muscle in Millimetres.	Extension.	
		In Man.	Per Cent.
0·3	24·9	—	—
1·3	30·0	5·1	20
2·3	32·3	2·3	7
3·3	33·4	1·1	3
4·3	34·2	0·8	2
5·3	34·6	0·4	1

Mansvelt, however, deduces as the principal result of his experiments, that living muscle is, at least within certain limits, extended in proportion to the increase of the weight, each fibre elongating about 1 per cent. of its length for each 65th of a grain weight appended to it. According to Wundt, the weight which is required to extend a fresh muscle of 1 square millimetre (1-25th of an inch) sectional area, twice its length, is 2 oz. The importance of the elasticity of the muscles is obvious, for by its means, notwithstanding that the distance between the points of origin and insertion is undergoing constant change, the muscles are kept in a state of constant slight tension, so that no time is lost before contraction begins; moreover, it prevents rupture both in sudden passive extension, and, which is far more important, when the muscle itself shortens, so that contraction is gentle and distributed over a longer time. As a rule, during life the muscles are subjected to strong but brief extension acting upon them when they are in a state of contraction, rather than in a state of relaxation. It would obviously have seriously interfered with their action had a high degree of elasticity been conferred upon them, since antagonistic muscles would have had this, in addition to all other

the true amount, and again, on being released from the weight, they quickly retract to a certain degree, and move slowly to their full extent. This constitutes the "elastische nachwirkung" or "secondary elasticity" of the Germans. This occasions much loss of time, and as the quality of the muscle rapidly changes, materially interferes with comparative experiments.

* Heidenhain, "Studien," Berlin, 1856; and Wundt, Müller's "Archiv," 1857.

† Schmulowitsch, "Centralblatt," 1870, p. 609.

‡ See a Review of his work in the "Med.-Chir. Rev." for 1864, p. 443, vol. i.

§ Wagner's "Handwörterbuch," Band iii. p. 54. See also Volkmann, Pflüger's "Archiv," Band vii. 1873, p. 15. Fick, Pflüger's "Archiv," 1871, Band iv. p. 301, finds that the elasticity of muscle varies with each degree of contraction.

resistances, to overcome, before movement could be effected. Weber has shown that the extensibility of muscles increases during contraction. He applied a weight of 115 grains to an elongated muscle. On the addition of another weight of 15½ grains, the amount of extension which took place was about 1–144th of its length; but on repeating the same experiment with a contracted muscle, the extension was as much as 1-79th of its length, showing that the extensibility was greater in the latter case than in the former. The exhaustion of a muscle greatly increases its extensibility up to a certain point, after which it again diminishes. Thus, when a portion of muscle was weighted with 115 grains, its greatest extension occurred when it had been made to contract 43 times; when weighted with 193 grains, after 23 contractions; and lastly, when weighted with 424 grains at the 8th contraction. It was even found that, by appropriate weighting, a muscle on being stimulated to contract might actually become longer instead of shorter.

623. *Electrical Relations of Muscle.*—As we have already seen in the Nerves (§ 426), so in the Muscles it is easy to furnish evidence of electrical disturbance. The conditions of the 'Muscular current' have been made the subject of special investigation by M. du Bois-Reymond; and the following is an outline of the results at which he has arrived, for the due comprehension of which, however, it is requisite that the terms employed by him should be first defined.—The entire muscle being composed of a mass of fibres, having a generally parallel direction, and attached at their extremities to a tendinous structure (which has in itself but little or no electro-motor power, but is a conductor of electricity), it follows that the tendon or tendinous portion of a muscle represents a surface formed by the *bases* of the muscular fibres considered as prisms, which may be designated its *natural transverse section.* On the other hand, the fleshy surface of the muscle, which is formed only by the *sides* of the fibres considered as prisms, may be regarded as the *natural longitudinal section* of the muscle. Again, if a muscle be divided in a direction more or less perpendicular to its fibres, an *artificial transverse section* will be made, whilst if the muscle be torn lengthways in the direction of its fibres, an *artificial longitudinal section* will be made; and these artificial sections show the same electric conditions with their corresponding natural sections. Now, experiments repeated in a great variety of modes demonstrate that *every point in the natural or artificial longitudinal section of a muscle is positive in relation to every part of its transverse section, whether natural or artificial;* and hence a current is passing in the muscle from the transverse to the longitudinal section (Fig. 197). The most powerful influence on the galvanometer is produced when a portion of the surface (or natural longitudinal section) of a muscle is laid upon one of the electrodes, and a portion of the surface formed by cutting the muscle across (or artificial transverse section) is placed against the other. When the two tendinous extremities of a muscle, whose form is symmetrical or nearly so, are placed against the electrodes, the deflection of the needle of the galvanometer is but slight; and the same is the case with two transverse sections taken at equal distances from the two ends of the muscle, and also with two points of the longitudinal section which are equally distant from the middle of its length. But if the two points of the longitudinal section applied to the electrodes be not equally distant from the centre of the muscle, then the point which is nearest to the centre is positive to the one which is nearest to the end; and, in like manner, when the different parts of the transverse section are tested in regard to each other, the points lying nearest the surface of the muscle are found to be positive to those nearest its anterior. The intensity of the current,

however, between any two points in the *same* section—whether transverse or longitudinal—is always incomparably less than that of the currents which are obtained between two points in *different* sections, one in the longitudinal and the other in the transverse. These results may be obtained, not merely with the entire Muscle, but with insulated portions of it; and even, as we are assured by M. du Bois-Reymond, with a single primitive fasciculus. It has been suggested by Hermann that the key to the electrical opposition which exists between the artificial transverse and the artificial longitudinal section is probably to be found in the action of oxygen on the muscular tissue, the surface exposed by the cut being more rapidly acted on, as compared with the longitudinal section, which is protected by more or less fascia, and by the sarcolemma of the fibres. In favour of this view it is to be observed that the more rapidly after removal from the body the electrical relations of the *natural longitudinal* and *artificial* transverse sections, or in other words of the tendon and the surface of the muscle are tested, the slighter is the difference found to exist between them; indeed, if the examination be made sufficiently early, especially if the animal has been kept in the cold, it will be found either that no difference exists between them, or that the tendon and a portion of the muscle near its longitudinal axis are positive in regard to the surface of the muscle.

624. *Negative Variation.*—That a change in the electric state of a Muscle takes place in the act of contraction, had been ascertained by the experiments of Professor Matteucci;* but as he was only able to detect this by the galvanoscopic frog (the galvanometer which he employed not giving unquestionable indications of it), he was not able to determine its nature with accuracy. This has been accomplished, however, by M. du Bois-Reymond; who has shown that during contraction the muscular current is not increased (as supposed by Matteucci), but is diminished, and even reduced to zero. In order to exhibit this phenomenon satisfactorily, it is found advantageous to cause the muscle to contract powerfully or uninterruptedly for as long a time as possible—that is, to *tetanize* it; and this may be effected by acting violently on its nerve by heat, chemical agents, or a rapid succession of electric shocks; or by poisoning the animal with strychnia. In whatever mode the tetanized state is induced, the same result follows—the needle of the galvanometer passes over to the negative side. Ranke† has noticed the remarkable fact that dead muscle is a better conductor of electricity than living, and that the conducting power of muscle exhausted by exercise is also increased. This he attributes to the accumulation of the products of disintegration, and especially to that of lactic acid. Living muscle conducts electricity about three millions times worse than mercury, and fifteen millions times worse than copper.

625. The rapidity with which the mandates of the Will are communicated to and executed by the Muscles is immeasurable; but Helmholtz has shown that if an electric spark, whose duration does not exceed one six- or seven-hundredth of a second, be allowed to strike a portion of fresh muscle, a measurable period, amounting to 1 or 2-100ths of a second, intervenes before the commencement of contraction. This he terms the *period of latent contraction or excitation.* At the commencement of the contraction which succeeds, an instantaneous electrical discharge occurs, lasting less than the 1000th of a second, and comparatively weak, but still probably equivalent to that of the electric organ in fishes.‡ The contraction which then takes place

* See his successive Memoirs in "Phil. Trans.," for 1845, 1847, and 1850.

† "Tetanus," Leipzig, 1865.

‡ See Donders' "Essay on the Constituents of Food," translated by Dr. Moore, Dublin, 1866, p. 14, where it is quoted as the observation of Meissner, and as corroborated by v. Bezold.

is not sudden and complete, but is divisible, according to Klünder,* into four stages, in the first of which the movement of contraction commences and slowly increases; in the second there is great increase in the rapidity of the contraction; the third is the period of maximum rapidity, and in the fourth there is a diminution of the rapidity. The first period can be much protracted by heavy weighting, and the last period is very variable. Klünder gives as the duration of the latent excitation of fresh and lively muscle $\frac{3}{400}$ths of a second, but when exhausted and heavily weighted it rises to $\frac{1}{100}$th of a second; previous extension of the muscle diminishes the duration of the latent excitation, as Helmholtz also found.† The true curve of contraction at its middle portion represents a parabola modified by the elasticity of the muscle. The period of time which elapses from the instant that the stimulus is applied until the contraction is complete, increases generally with the amount of shortening, with the heaviness of the weight, and with the exhaustion of the muscle. In the Frog the entire time occupied in the contraction and subsequent elongation of a muscle is about one-third of a second, of which

Fig. 293.

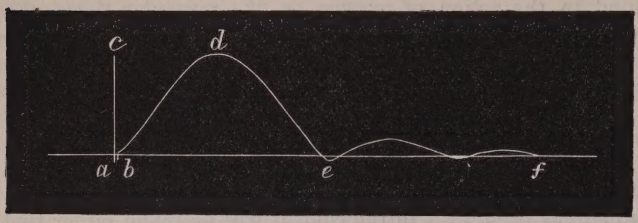


Diagram of a muscle curve as drawn on a travelling surface. *a d e f* the line described by the point of the lever connected with the muscle; *a*, the base line. The vertical line, *a c*, marks the moment of stimulation; *b*, the beginning, *d*, the maximum, and *e*, the end of the contraction of the muscle. The interval between *a* and *b* is known as the "latent period" of the contraction of the muscle. The undulations between *e* when the contraction of the muscle has ceased, and *f*, are believed to be due to the elasticity of the muscle.

	Of a second.
The period of latent excitation amounted to	0·02
„ „ contraction „	0·180
„ „ elongation „	0·105
	·305‡

From the results of various experiments, Helmholtz satisfied himself that to develop their greatest force, muscles require a longer time than when slight efforts only are made.§

626. *Mechanism of Muscular Contraction.*—From the inquiries of Mr. Bowman, it appears that the act of contraction usually commences at the extremities of the fibre; but it frequently occurs also at one or more inter-

* Op. cit., p. 129.

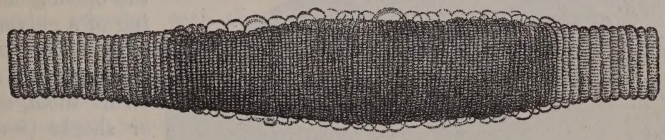
† Ranvier ("Comptes Rendus," lxxvii. p. 1105, and "Archiv. de Physiolog.," t. vi. p. 1) has pointed out various differences between the white and the red muscles of the rabbit, and amongst others, that the period of latent excitation of the white muscles of the rabbit is 1-83rd of a second, whilst for the red muscles it is as much as 1–18th of a second.

‡ See Helmholtz in Müller's "Archiv," 1850, 1852; and Volkmann, in "Leipzig. Berichte Math. Phys. Class.," 1851. Place has more recently ("Nederland. Archief," Band iii. 1867, Heft 2) estimated the period of latent excitation in the muscles of frogs at only 0·005 sec., and he finds the rapidity of propagation of the excitation through muscles to be about one metre per second.

§ For a very minute investigation on this point, see Klünder, 'Ueber den zeitlichen Verlauf der Muskelzuckung,' in the "Arbeiten aus dem Kieler Physiologischen Institut.," 1868, pp. 107–130.

mediate points. The first appearance is a spot more opaque than the rest, caused by the approximation of a few of the dark points of some of the fibrillæ; this spot usually extends in a short time through the whole diameter of the fibre; and the shading caused by the approximation of the transverse striæ increases in intensity. The striæ are found to be two, three, or four times as

Fig. 294.



Muscular Fibre of Dytiscus, showing the *contracted state* in the centre; the striæ approximated; the breadth of the fibre increased; and the sarcolemma raised in bullæ on its surface.

numerous in the contracted as in the uncontracted part, and are also proportionally narrower and more delicate. The line of demarcation between the contracted and uncontracted portions is well defined; but as the process goes on, fresh striæ are absorbed as it were from the latter into the former. The contracted part augments in thickness, but not in a degree commensurate with its diminished length, so that its solid parts lie in smaller compass than before—the fluid which previously intervened between them being pressed out in bullæ under the sarcolemma (Fig. 294). Marey and Aeby have shown that when a muscle is excited by passing a current of electricity through it, every part contracts simultaneously, as proved by the identity in point of time of tracings taken with levers attached to different parts. In like manner, when the nerve supplying a muscle is excited, the whole muscle appears to contract simultaneously, and this is explained by Aeby on the supposition that the contraction commences at the point of entry of each terminal twig of the nerve, and propagates itself away from this point in both directions. As these points of entry are distributed very irregularly in neighbouring fibres, the swelling appears to be uniform throughout. In one of his experiments, a muscle of a frog is taken, the motor nerve of which bifurcates as it enters. One of the divisions is cut, and the main trunk excited. It is then found that that portion of the muscle which is supplied by the intact nerve contracts simultaneously throughout, whilst in the remaining portion a wave is propagated that travels at precisely the same rate as the contraction that occurs when mechanical irritation is applied to a given point of a fresh muscle. The rapidity of this last is given by Aeby,* for the muscles of frogs at about 40 inches per second, Bernstein† estimated it far more highly at nearly 13 feet per second, and quite recently Hermann‡ operating on the muscles of frogs, both with and without curare, gives the rapidity at 2·698 metres per second, or about 9 feet. It is increased by heat and retarded by cold. M. Marey§ has lately shown by means of his delicately constructed registering apparatus, that the contraction of a muscle which follows the application of a sudden stimulus, as of an electric spark, differs remarkably from the contraction

* "Untersuchungen über Fortpflanzungsgeschwindigkeit der Reizung," &c., Braunschweig, 1862. See also v. Bezold, Meissner's "Jahresbericht," 1860, p. 482; Engelmann, "Jenaische Zeits.," Band iv. p. 305; Place, "Onderzoek. ged. in het Phys. Lab. der Utrecht. Hoogeschool," Band ii. Recks i. p. 135; Valentin, Pflüger's "Archiv," Band iv. p. 115.

† "Untersuchungen," &c., Heidelberg, 1871, p. 76.

‡ Pflüger's "Archiv," Band x. 1875, p. 54. See also Jendrassik, "Archiv f. Anat. u. Physiol.," 1874, p. 513, who gives a lower estimate—viz., from 0·524 m. to 1·154 m.

§ See his Lectures on 'Self-registering Apparatus,' in the "Revue des Cours Scientifiques," tom. iii.

induced by a voluntary impulse. In the former instance the contraction is sudden and single, especially if the muscle be quite fresh, becoming slower as the muscle experiences fatigue. This is clearly shown in the following woodcut, which represents the tracing obtained on a rapidly-rotating circular disk from a muscle made to contract by the opening and closing of a galvanic current. Two contractions, or, as M. Marey terms them, impulses or shocks (secousses) are exhibited. One series (o) corresponding to the period of opening of the induced current, the other of closing (C). The line traced at the bottom of the figure by a diapason vibrating 100 times (double vibrations) per second enables the duration of each of the impulses to be estimated. The arrangement of the apparatus is such that the lower lines represent the tracing obtained when the muscle is in the perfectly recent state, whilst the upper ones represent it when more or less exhausted. It will be noticed that for each galvanic shock there is a single instantaneous contraction represented by an elevation with rounded summit, and that the period of ascent corresponding to the period of shortening of the muscle (on the left) is more rapid than the period of descent of the line, the latter corresponding to the period of relaxation. In proportion as the muscle becomes fatigued, three peculiarities may be noticed: the duration of the contraction or shock augments; the period of ascent becomes prolonged, and the height of the wave or amount of shortening of the muscle increases. This last, however, is only transient, since, if the tracings be continued, the wave height diminishes though its width continues to increase. The tracings present the same features whether the excitation be applied to the nerve supplying the muscle, or to the muscle itself. It is very interesting to remark that the phenomena of exhaustion are not produced in the living body within moderate limits, indicating that reparation is constantly taking place. Of all the muscles of the body, the heart alone in its ordinary contraction gives a tracing corresponding to that obtained from a voluntary muscle on the application of an electrical shock—that is to say, the heart constitutes the only instance where each contraction is definite and single, and it presents the same characters in all animals. In all other instances, what is termed a muscular contraction consists of a series of shocks or impulses, as shown in Fig. 296, in which a tracing is shown such as may be obtained from a muscle caused to contract by a voluntary effort, or to which excitations at regular intervals are applied. Here the effects of the successive shocks are in the first instance superadded to one another till a

Fig. 295.

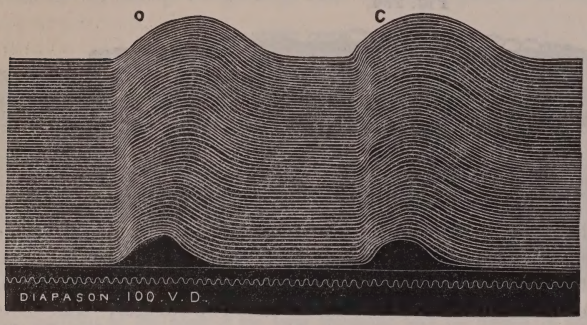
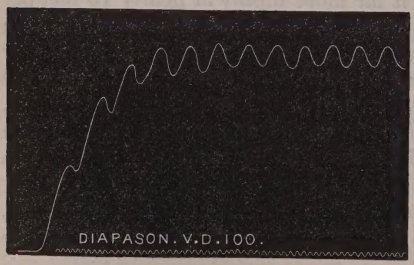


Fig. 296.



certain degree of contraction is obtained, which remains permanent with that amount of stimulation. If the electrical or mechanical* excitations are made to succeed each other more rapidly (Fig. 297), the successive shocks unite more quickly and completely, and the total contraction is greater in degree. Finally, if the excitations are repeated more than a certain number of times per second, varying with the animal and the state of the muscle, the several shocks fuse completely into one another, and tetanus is produced in which no vibration is perceptible (Fig. 298). The muscles of different animals respond differently to electrical excitation. In the case of the bird,† permanent contraction or tetanus is not produced until more than 75 shocks are communicated in a second, whilst the muscles of a tortoise are tetanized with only three shocks per second. Ranvier‡ found considerable difference in the reaction of the white and red muscles of rabbits to induced electricity. Thus the semi-tendinosus (a red muscle) excited for one-seventh of a second with a current that was interrupted 357 times in a second, passed at once into a state of tetanus (Fig. 298, c) and its myographic tracing exhibited a continuous and uniform elevation. The adductor longus, on the other hand (a pale muscle), stimulated in the same way, showed as many elevations and depressions as there were interruptions of the current (Fig. 297).

Fig. 297.

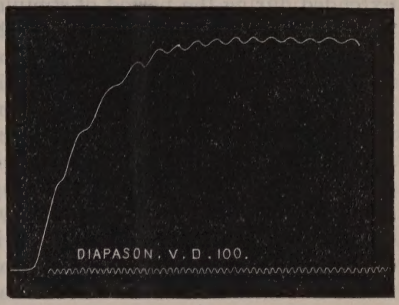
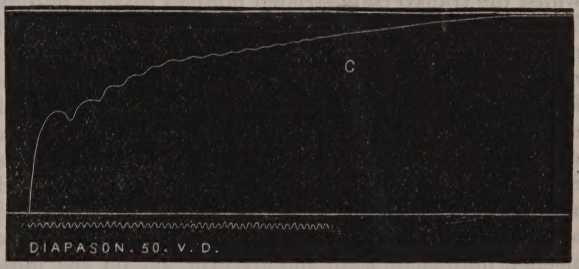


Fig. 298.



627. The contractility of the muscles may be called into play either directly by stimuli applied to the tissue itself, or indirectly by agents exciting the motor nerves. The contraction which follows in the latter instance is termed by Schiff *neuro-muscular*, and in the striated muscles is sudden, general, and energetic; but when mechanical irritation is directly applied to a muscle, the tissue itself responds to the stimulus, producing what Schiff has termed *idio-muscular* contraction. It may be observed in the manner first described by Dr. Stokes§ by percussing the pectoralis muscle of emaciated patients, or by drawing the back of a knife across a muscle after all signs of irritability on the application of stimuli to the motor nerve have ceased; it then presents itself as a swelling or intumescence a few lines broad and high, but varying with the strength of the blow, lasting for four or five seconds, and slowly disappearing. Kronecker and Stirling‖ found that the red muscles of the rabbit,

* As in Heidenhain's mechanical Tetano-motor, in which a little hammer is set in motion by an electro-magnetic current, and a tetanic condition can be established in the muscles which will last for two minutes or more, till the irritability of the nerve is destroyed.

† Marey, "Rev. des Cours Scient.," vol. iv. 1867, p. 215.

‡ Brown-Séquard's "Archives de Physiol.," 1874, t. vi. p. 5.

§ "On Diseases of the Chest," p. 397. ‖ Foster's "Journal of Physiology," vol. i. p. 395.

when stimulated with four shocks per second, passed into incomplete tetanus; and with ten shocks per second into complete tetanus. The pale muscle of the rabbit requires 20-30 shocks per second to be completely tetanized, whilst six induction shocks per second prevent it from becoming completely extended during the period of stimulation. A further phenomenon has been noticed in the same muscles by Auerbach* after an energetic blow; namely, a wave or undulating contraction, proceeding from either side of the local intumescence of Schiff, and propagating itself to the extremity of the muscle at the rate of about eighteen inches per second. The breadth of the waves is about a quarter of an inch at their base, and they gradually die out as they spread from the point struck. It is doubtful whether both of these appearances are not due simply to a prolonged contraction of the muscle, resulting from exhaustion of its contractility at the excited spot. A difference of opinion exists in regard to the activity of the circulation in muscle during contraction; Ludwig and his pupils maintaining that it is accelerated, whilst Bernard considered that it was nearly arrested.

628. The unstriated muscles of different animals react differently to heat.† The smooth muscular tissue of the bladder of the Frog elongates on being warmed, and shortens on being cooled, but the opposite occurs with the smooth muscular tissue of the rabbit and cat; nevertheless, if long kept at a high temperature the unstriated muscles of warm-blooded animals gradually relax, whilst the transversely striated muscles passing into rigor, remain shortened. The striated muscle of the frog, when excised and suddenly exposed to a temperature of 77° F., undergoes slow shortening; at 86° F., the shortening becomes more marked; and at 113° F., reaches its maximum. v. Bezold‡ and Prevost have found that in a certain stage of Veratrin poisoning the muscles respond to a single electric shock, not with a single short contraction, but with a persistent tetanic contraction; and, according to Weyland, the same results from the action of Sabadillin, Delphinin, Emetin, and Aconitin.§ As regards chemical agents, some appear to act with equal energy in producing contraction, whether applied to the muscle or to the motor nerve, as solutions of potash and soda; others, as creosote, alcohol, pure lactic acid, and glycerin, act on the muscle through the nerve, but possess little stimulating power when directly applied to the muscle; and others again excite energetic contraction when made to act immediately on the muscle, but scarcely operate through the nerve, as sulphate of copper and ammonia.‖ Kühne¶ remarks that all those bodies which coagulate the muscle plasma, as dilute acids and alkalies, act as powerful stimulants to muscles even when very dilute. The metallic salts, as a rule, require to be in a stronger state of concentration. He thinks that each part as it contracts, generates material (paralactic acid) which again acts as an excitor to the next adjoining layer.

629. Muscular Irritability is deadened by many substances, and especially by those which have a narcotic or sedative action on the nervous system. In carbonic acid gas, hydrogen, carbonic oxide, or sulphurous acid gas, muscles contract very feebly, or not at all, when stimulated; whilst in oxygen they

* "Abhand. der Schleswig. Gesellsch.," 1861, p. 294.

† Schmulewitsch, Samkowry, Pflüger's "Archiv," Band ix. p. 399.

‡ "Centralblatt," 1869, p. 600.

§ See for an extensive series of researches on this point, including the action of Tartar Emetic, Upas Antiar, Caffein, Chloroform, Napellin, Quinin, and other drugs, Buchheim and Eisenmenger in Eckhard's "Beiträge zur Anat. u. Physiol.," Band v. 1871, p. 73.

‖ See Dr. Duffin's paper 'On Muscular Contraction,' in Beale's "Archives of Medicine," vol. iii. p. 147; and Kühne in "Archiv f. Anat. und Physiologie," 1859, p. 213.

¶ "Physiol. Chemie," 1868, p. 311.

retain their irritability longer than usual. Narcotic substances, such as a watery solution of opium, when applied directly to the muscles, have an immediate and powerful effect in diminishing or even destroying their irritability; this effect is also produced, though in a less powerful degree, by injecting these substances into the blood. In the same manner venous blood charged with carbonic acid, and deficient in oxygen, has the effect of a poison upon the muscles, diminishing their irritability, when it continues to circulate through them, to such a degree that they sometimes lose it almost as soon as the circulation ceases, as is seen in those who have died from gradual and therefore prolonged asphyxia. The unfavourable influence of venous blood is also shown in the Morbus Cœruleus, patients affected with which are incapable of any considerable muscular exertion. Although most of the stimuli which occasion the contraction of muscles, when directly applied to their fibres, operate also when applied to their motor nerves, the same does not hold good in regard to those agents which diminish irritability. It is a fact of some importance in relation to the disputed question of the connection of muscular irritability with the nervous system, that when, by the application of narcotic substances to the nerves, their vital properties are destroyed, the irritability of the muscle may remain for some time longer, showing that the latter must be independent of the former.—The effects produced by the Curare and Upas Antiar poisons in this respect are exceedingly curious, and have been carefully studied by Bernard* and others. Curare, Conia, and, as Drs. Crum Brown and Fraser† have shown, the Sulphates and Iodides of Methyl-Strychnium, Methyl-Brucium, Methyl-Thebaium, Methyl-Codeium, and Methyl-Morphium all act directly upon the motor nerves, whilst Cyanide of Potassium and the poison of the Upas Antiar abolish the irritability of the muscular tissue itself. The evidence given by Bernard in proof of this last statement is very satisfactory, for he has shown that the cause of death after the administration of a sufficient dose of Curare is the cessation of the respiratory movements owing to paralysis of the motor nerves; for not only has it been proved by v. Bezold that by this agent the rapidity of the conduction of stimuli through the motor nerves is greatly reduced and ultimately abolished, but it is certain that perfect recovery may take place if artificial respiration be maintained for a sufficient length of time to enable the poison to be eliminated from the system or decomposed within it; whilst in fœtuses, and during the earlier stages of existence of fishes and other animals that are not directly dependent upon muscular movements for the aëration of their blood, this being accomplished by the umbilical vesicle, little or no injurious effect is experienced, the animals continuing to swim about in a watery solution of the poison without apparent inconvenience. That the sensory nerves are not affected, seems to be proved by the experiments of Kölliker and Funke, who observed that reflex actions could readily be excited in parts kept free from the circulation of poisoned blood by the ligature of their vessels, on pricking or pinching the skin of parts poisoned by the admission of blood containing Curare. The influence of the poison seems to be first felt by the peripheral extremities of the motor nerves, and its paralyzing effect gradually extends centripetally through the trunks.—An additional argument may be mentioned in favour of the essential independency of muscular irritability, in the circumstance that,

* See his Lecture in "Med. Times and Gazette," 1860, vol. ii.; also A. v. Bezold in "Monatsbericht der Berlin. Akad.," 1859; and Martin-Magron and Buisson in "Journal de la Physiologie," 1860.

† "Transact. of the Roy. Soc. of Edinb." 1868. A paper of great value on the connection between chemical constitution and physiological action.

although spontaneous movements occur in the muscles of embryos, the muscles cannot, in the earlier periods of fœtal life, be incited to contract by stimuli directly applied to their nerves.—Dr. Harless* again found that when the Nervous system had been rendered, by the inhalation of ether, utterly incapable of conveying a galvanic stimulus applied either to the nervous centres or to the nerve-trunks, the same stimulus applied directly to the muscles would immediately throw them into powerful contraction. Various other experimenters have shown that when the nerves supplying the muscles of a limb are divided and the animals are allowed to live, excitants applied to the nerves beyond the point of division fail to produce muscular contraction long before they cease to do so when applied to the muscles themselves. Hence it is obvious that the activity of the Nervous system is not essential to the manifestation of the characteristic endowment of the Muscular.

630. The contractions of the Heart present some differences from those of ordinary striated muscular tissue, probably depending upon the peculiar arrangement of its fibres, whereby the contraction of one set gives a mechanical stimulation to others; for the muscular substance of a large part of the organ is thrown into rapid and energetic contraction by a stimulus applied at any one point, and this contraction is speedily followed by relaxation, which is again succeeded by a number of alternating contractions and relaxations.† Each contraction, however, has been shown to be equivalent to a single shock in an ordinary striated muscle (§ 626). On the other hand, if we apply a similar irritation to a portion of non-striated fibre, as that of the Intestinal Canal, the fasciculus which is stimulated will contract less suddenly, but ultimately to a greater amount; its relaxation will be less speedy, and before it takes place, other fasciculi in the neighbourhood begin to contract; their contraction propagates itself to others, and so on. In this manner consecutive contractions and relaxations may be produced through a considerable part of the canal by a single prick with a scalpel. Again, in the muscular structure of the Bladder and Uterus (when the latter is fully developed), direct irritation excites immediate and powerful contractions, which extend beyond the fasciculus actually irritated, and produce a great degree of shortening; but they do not alternate in the healthy state with any rapid and decided elongation. Similar phenomena may be observed on irritation of the smaller arteries. In order to obtain the full contraction of a muscle by irritation applied to the nerves, it is requisite that the stimulus should be applied for a certain length of time; thus Budge‡ found that when an electric current was passed through the cervical region of the spinal cord of a rabbit for the space of half a second, the pupil dilated about one-sixth of an inch; but on continuing the application for three seconds, dilatation occurred to the extent of nearly one-third of an inch. In all cases relaxation speedily alternates with contraction, unless the operation of the stimulus be continued—as when an electric current is propagated without intermission along the nerve trunks—in which case the contraction lasts as long as the stimulus is continuously applied but ceases as soon as it is withdrawn. The singular "inhibitory" effects produced by irritation of some nerves, as the pneumogastric and splanchnic, have already (§§ 98, 226, 239) been alluded to; but further experiments are still required before it can be admitted that any nerve can really transmit a "stimulus to relaxation" on the part of the muscle to which it is distributed. The general fact that relaxation alternates with contraction at no long intervals

* Müller's "Archiv," 1847, Band ii.

† Ray Lankester (Pflüger's "Archiv," 1871, p. 315) has shown that the muscular tissue of the Heart is characterized by containing hæmoglobin. ‡ "Physiologie," 1862, p. 650.

is most evident in the rhythmical movements of the Heart,* and in the peristaltic action of the Intestinal Canal; since in these parts the whole or a large proportion of the fibres seem to contract together, and then shortly relax. But this is probably no less true of the individual fibres of those muscles which are kept in contraction by a stimulus transmitted through their nerves; since none of them appear, under ordinary circumstances at least, to remain in a contracted state for any length of time, a constant interchange of condition taking place among the fibres, some contracting while others are relaxing, and *vice versâ*. It is difficult to speak with confidence, however, in regard to the condition of the individual fibres of a muscle that is thrown into a state of *continued spasmodic* contraction. Whether the individual fibres in such instances maintain a state of contraction without intermission, or whether the contraction of the entire muscle is kept-up by a continual interchange of the fibres actually engaged, is a very curious subject for inquiry.

631. Muscles do not lose their Irritability immediately on the *general death* of the system, which must be considered as taking place when the circulation ceases without the power of renewal; in cold-blooded animals it is retained much longer after this period than in the higher Vertebrata, in some instances attaining its highest degree long after death has occurred,† whilst in the latter it frequently disappears within an hour. The muscles of young animals generally retain their irritability for a longer time than those of adults; on the other hand, those of Birds lose their irritability sooner than those of Mammalia. Hence, as a general rule, the duration of the irritability is inversely as the amount of respiration. From experiments on the bodies of executed criminals who were previously in good health, Nysten ascertained that in the Human subject the irritability of the several muscular structures disappears in the following time and order:—The left ventricle of the heart first, the intestinal canal at the end of 45 or 55 minutes, the urinary bladder nearly at the same time, the right ventricle after the lapse of an hour; the œsophagus at the expiration of an hour and a half, the iris a quarter of an hour later; the muscles of animal life somewhat later; and lastly, the auricles of the heart, especially the right, which in one instance contracted under the influence of galvanism 16½ hours after death. It will be presently shown that the departure of the irritability is essentially dependent upon the cessation of the circulation, and that it may be prevented from disappearing, and may even be recalled after it has ceased to manifest itself, by transmitting a current of arterial blood through the muscles. Kronecker‡ has endeavoured to establish

* Some curious rhythmical movements have been observed by M. Brown-Séquard ("Gaz. Med.," 1849) in the diaphragm, in the intercostals, and in some of the muscles of locomotion, both after death and after section of their nerves during life. These movements could not be in any way dependent upon reflex action, because they took place when the muscles were completely cut off from the nervous centres, sometimes to the number of from 5 to 20 in a minute, and for as long as a quarter of an hour after death; and occasionally recurred in living animals for many months afterwards, especially when the respiration was impeded and the circulation hurried. Of a similar nature are the vibratory movements of the muscles of the tongue witnessed by Schiff after section of the Hyoglossals ("Physiologie," 1859, p. 177); and we may perhaps refer to the same category the trembling movements of the hands and head in old age, in certain forms of paralysis, and in habitual drunkards and smokers. All these cases furnish evidence of a tendency to rhythmical movements in the muscles themselves, altogether independent of the excitement to action which they receive through the nervous system.

† See on the whole subject of the 'Irritability of Muscles,' a good paper by Dr. Norris in Humphry and Turner's "Journ. of Anat.," vol. i. p. 217. See also B. W. Richardson's 'Croonian Lecture on Muscular Irritability after Systemic Death,' Abst. in "Lond. Med. Record," June 18, 1873.

‡ See abstract of his paper in the "Journal of Anatomy and Physiology," vol. vi. 1872, p. 241.

certain laws of muscular exhaustion to this effect :—1. That if a muscle be overloaded with a definite weight, and irritated at equal intervals by equal induction shocks, the height of the contractions form an arithmetical series, in which the constant difference depends only on the interval of time. 2. The diminution in the height of the contractions is independent of the weight, and only depends on the interval between two contractions.*

632. We find, however, that sudden and severe injuries of the Nervous centres have power to *impair*, directly and instantaneously, or even to *destroy* the contractility of the whole Muscular system; so that death immediately results, and no irritability subsequently remains. It is in this manner that the *sudden* destruction of the brain and spinal cord, especially of the latter, occasions the immediate cessation of the heart's action, though they may be *gradually* removed without any considerable effect upon it. Severe concussion has the same effect; hence the syncope which *immediately* displays itself. It is sometimes an important question in forensic medicine, whether an individual who has died from the effects of a blow upon the head, could have moved from the place where the blow was inflicted. If there be found, as is frequently the case, no sensible disorganization of the brain, the death must be attributed to the concussion, and must have been in that case *immediate*. If, on the other hand, effusion of blood has taken place within the cranium to any considerable extent, it is probable that the first effects of the blow were in some degree recovered from, and that the circulation was re-established. It is not essential, however, that the impression should be primarily made upon the Cerebro-Spinal system. The well-known fact of sudden death not unfrequently resulting from a blow on the stomach, especially after a full meal, without any perceptible lesion of the viscera, clearly indicates that an impression upon the widely-spread cœliac plexus of Sympathetic nerves (which will be much more extensively communicated to them when the stomach is full than when it is empty) may cause the immediate cessation of the heart's action in the same manner as a violent injury of the brain or spinal cord.† In all these cases *the whole vitality* of the system appears to be destroyed at once; for the processes which would otherwise succeed to the injury, and which after other kinds of death less sudden in their character, produce evident changes in the part of the surface that has immediately received it, are here entirely prevented. An instance is on record in which a criminal under sentence of death determined to anticipate the law by self-destruction. Having no other means of accomplishing his purpose, he stooped his head and ran violently against the wall of his cell; he immediately fell dead, and *no mark* of contusion showed itself on his forehead. The same absence of the usual results is to be noticed in the case of blows on the stomach. The influence of severe impressions on the nervous system in *diminishing*, when it does not altogether destroy, muscular irritability, is well seen in the operation of severe injuries affecting vital organs, or extending over a large part of the surface, in depressing the heart's action; to which attention has already been directed (§ 222).

633. From a general consideration of the phenomena of Irritability, we can scarcely do otherwise than acquiesce fully in the doctrine of Haller, which involves no hypothesis, and which is perfectly conformable to the analogy of other departments of Physiology. He regarded every part of the body which is endowed with irritability as possessing that property in and by itself; but considered that the property is subjected to excitement and control from the

* See, in regard to the irritability of muscles after systemic death, B. W. Richardson, "Proceed. Roy. Soc." 339, 1874.

† For examples of this see "Lancet," 1870, vol. i. p. 276.

nervous system, the agency of which is one of the stimuli that can call it into operation. It may be desirable briefly to sum up the facts by which this doctrine is supported. 1. The existence in vegetables of irritable tissues, which are excited to contraction by stimuli directly applied to themselves, and which can be in no way dependent upon or influenced by a nervous system. 2. The existence in animals of a form of muscular tissue which is especially connected with the maintenance of the organic functions, and which is much more readily excited to action by direct stimulation than it is by nervous agency. 3. The fact that by the agency of these the organic functions may go on (so long as their requisite conditions are supplied) after the removal of the nervous centres (of the Cerebro-Spinal system at least), and when these were never present; rendering it almost certain that their ordinary operations are not dependent upon any stimuli received through the nerves, but upon those directly applied to themselves. 4. The persistence of irritability in muscles, for some time after the nerves have ceased to be able to convey to them the effects of stimuli: this is constantly seen in regard to the Sympathetic system of nerves, and the muscles of organic life upon which they operate; and it is shown, by the agency of narcotics, to be true also with respect to the Cerebro-Spinal system and the muscles of Animal life. 5. The continuance of irritability in the muscles after their complete isolation from the nervous centres, so long as their nutrition is unimpaired; and the effects of frequent exercise in preventing the impairment of the nutrition and the loss of irritability. 6. The recovery of the irritability of muscle, when isolated from the nervous centres, after it has been exhausted by repeated stimulation: this also depends upon the healthy performance of the nutritive actions. 7. The existence of certain poisons which appear to possess a directly depressing effect on the conducting power of motor nerves, without exerting any influence upon the irritability of muscles (§ 629). 8. The existence of certain tracts of muscular tissue, as those, for instance, of the walls of the umbilical vessels, which according to Virchow, whilst possessing considerable irritability, show no trace of nervous tissue. In the words of Dr. Alison, then, "the only ascertained final cause of all endowments bestowed on nerves in relation to muscles in the living body, appears to be not to make muscles irritable, but to subject their irritability in different ways to the dominion of the acts and feelings of the mind"—to its volitions, emotions, and instinctive determinations.*

634. The experiments of Mr. Gaskell† show that the flow of blood through muscles undergoes considerable variation under different circumstances. In muscles at perfect rest, with untouched nerves, the flow of blood from the veins is nearly absolutely regular. After section of the nerve supplying a muscle, the flow of blood through its vessels is immediately and greatly increased, probably owing to the division of the vaso-motor nerves and loss of tone in the vessels, but this effect is only temporary, and the flow falls to its normal amount. In some instances there is a secondary and more permanent rise on stimulation of the nerve, so as to produce tetanus. There is at first a spurt-like quickening of the stream, followed by an almost complete cessation of the flow, which then again steadily increases in volume. At the end of the tetanus the flow sinks for a moment, then rises to a new maximum, and finally falls to its original value. There can be no question that the condition most essential to the maintenance of muscular contractility is an *adequate supply*

* For a good *résumé* of the arguments for and against the theory of independent irritability in muscles, see a paper by Dr. H. N. Maclaurin in "Edinb. Med. Journal," July, 1863.

† "Journ. of Anat. and Phys.," vol. xi. 1877, p. 360.

of arterial blood. It is well known that when a ligature is applied to a large arterial trunk in the Human subject, there is not only a deficiency of sensibility in the surface, but also a partial or complete suspension of muscular power, until the collateral circulation is established. The same result has been constantly attained in experiments upon the lower animals; the contractility of the muscle being impaired or altogether extinguished when the flow of blood into it was arrested, and being recovered again when the supply of blood was restored.—The various experiments of Brown-Séquard* on this subject show that the contractility of muscles, whether of the striated or smooth variety, may not only be restored by the transmission of aërated blood through them, after it has entirely ceased, but that this may even occur when it has given place to cadaveric rigidity. Thus he found that when he connected the aorta and vena cava of the body of a rabbit which had been some time dead, and in which the cadaveric rigidity had already manifested itself for between ten and twenty minutes with the corresponding vessels of a living rabbit, so as to re-establish the circulation in the lower extremities, the rigidity disappeared in from six to ten minutes, and in two or three minutes afterwards the muscles contracted on being stimulated. He subsequently made similar experiments upon the muscles of a decapitated criminal; the hand being selected as a convenient part for the purpose. It was not until nearly $12\frac{1}{2}$ hours after death that all traces of irritability had left the muscles, and the injection was not commenced until 45 minutes after this, cadaveric rigidity having appeared in the interval. About half a pound of human blood, which had been defibrinated and freely exposed to the air so as to acquire the arterial tint, was then injected at intervals for about thirty-five minutes; ten minutes after the last injection, the greater number of the muscles were found to be irritable, and these remained so for two hours, after which the contractility gradually departed, and was succeeded by cadaveric rigidity. The blood which had been injected in an arterialized condition issued from the vessels quite dark; and as this occurred over and over again, the change of hue could not be attributed to anything else than the reaction between the blood and the tissues.—Similar experiments were made twenty-seven hours after death upon the muscles of the foot of the same criminal; but with an entirely negative result, save that the blood which was injected returned of a considerably darker hue.†—Still more recent experiments have shown that in order that the muscles should retain their elongated condition, it is necessary that they should be supplied with arterial blood, the passage of venous blood through their capillaries immediately inducing contraction. This was remarkably exemplified in an experiment made by M. Brown-Séquard upon a pregnant rabbit, in which the injection of venous blood into the uterine vessels immediately excited the organs to contract, and caused the expulsion of two or three fœtuses, whilst on injecting arterial blood all signs of contraction immediately passed off. It is doubtful whether

* See "Gazette Médicale," 1851, Nos. 24 and 27; and "Journal de la Physiologie," 1858, vol. i. pp. 95, 353, 729. For some more recent experiments, see M. Robin in his "Journal de l'Anatomie," 1869, p. 69.

† In Robin's experiments upon decapitated criminals, the heart could be made to recommence its rhythmical contraction by blowing air into its cavities upwards of one hour and a quarter after execution. The contractions continued for eight minutes. Rosenthal ("Wien. Med. Press," 1872, Nos. 18 and 19) found that the muscles of the trunk and extremities of man lose their irritability and cease to respond to farado-electrical excitation within a period varying from 90 to 180 minutes after death. In frogs the irritability of the muscles lasts for many hours when kept in a moist chamber. Newman, "Journal of Anat. and Phys.," vol. xiii. 1879, p. 573, found the fibres respond to the stimulus of an acid or alkaline solution 70 hours after the death of the animal.

the stimulus to contraction in these cases is the presence of carbonic acid, or whether, as Dr. Radcliffe* supposes, it is not rather to be attributed to a deficiency of oxygen, the readmission of which restores the vital properties of the muscle and induces its elongation. The latter view is certainly supported by the violent convulsions which occur in animals that are bled to death; and even the convulsions which are witnessed in asphyxia, when the contracted state of the small arteries (§ 300) and the consequent diminished transmission of blood through the capillaries are borne in mind, are not unfavourable to it. Dr. Radcliffe has adduced the interesting experiments of Dr. George Harley† upon the influence of the addition of strychnia and brucia to blood, as essentially confirmatory of his view; since these poisons diminish the capacity of the blood to absorb oxygen, and their action may thus be said to be equivalent to a copious loss of blood.

635. Whilst the Irritability of Muscles is gradually departing after death, it not unfrequently shows itself under a peculiar form; for, instead of producing sudden contractions, speedily followed by relaxation, the application of Stimuli then occasions slow and somewhat prolonged contractions, the relaxation after which is tardy. This form of contraction is seldom seen in adult Mammalia, except (as will be presently shown) when death has taken place from certain diseases that have a special influence on the blood and muscular system; but it is stated by M. Brown-Séquard‡ to present itself more constantly in young animals, and to be (so to speak) an exaggeration of the ordinary *modus operandi* of their muscles, which during life are much more slowly thrown into contraction by mechanical stimuli than they are in adults. —The most remarkable manifestations of it yet observed, however, have been witnessed after death from Cholera and Yellow Fever; for in these cases the muscular contractions, though capable of being excited by mechanical stimulation applied to the muscles themselves, are frequently spontaneous, and sometimes give rise to movements strongly resembling the ordinary actions of the living state. In regard to the occurrence of this phenomenon, after death from yellow fever, several interesting observations have been recorded by Dr. Bennet Dowler, of New Orleans.§ In one case, the subject of which was an Irishman, aged twenty-eight, the following series of movements took place spontaneously not long after the cessation of the respiration; first the left hand was carried by a regular motion to the throat, and then to the crown of the head; the right arm followed the same route on the right side; the left arm was then carried back to the throat, and thence to the breast, reversing all its original motions, and finally the right hand and arm did exactly the same. Similar phenomena have been described by Mr. N. B. Ward, Mr. Helps, and Mr. Barlow‖ as occurring in the bodies of cholera patients. Many circumstances indicate that these movements were due to the inherent contractility of the muscles, and were not in any degree dependent upon the operation of the nervous system; and Mr. Dowler proved experimentally, by completely separating limbs which exhibited these movements from the trunk of the body, that the influence of the nervous centers was not in any degree essential to their production.

636. The *Rigor mortis*, or Cadaveric rigidity of the muscles, is essentially

* In whose work "On Epileptic and other Convulsive Affections of the Nervous System" (3rd edit., 1861) much original and interesting information on the subject of muscular contractility will be found.

† See "Lancet," 1856.

‡ "Gazette Médicale," December 22, 1849. See also Norris, loc. cit.

§ "Experimental Researches on the Post-mortem Contractility of the Muscles," 1846.

‖ See Mr. F. Barlow's 'Observations on the Muscular Contractions which occasionally occur after Death from Cholera,' in "Med. Gazette" for 1849–50.

the result of the coagulation of myosin (which, according to Michelson, is due to the action of a ferment),* and is attended with the liberation of heat. It begins immediately after all indications of irritability have departed, but before any putrefactive change has commenced. The supervention of the rigidity is not usually prolonged much beyond seven hours, though a tetanic state at first sight resembling it may occasionally be observed to occur instantly after death from some peculiar conditions of the nervous and muscular systems at the moment. In other instances twenty or even thirty hours may elapse before it shows itself. Its general duration is from twenty-four to thirty-six hours, but it may pass off much more rapidly, or it may be prolonged to four or six days. It first affects the neck and lower jaw, then the trunk, then the upper extremity, and finally the muscles of the lower extremities. In its departure, which is immediately followed by decomposition, the same order is followed. It is remarkable that it is equally intense in muscles which have been paralyzed by Hemiplegia, or whose nerves have been previously severed, provided that no considerable change has taken place in their nutrition. It was the opinion of Mr. Hunter that death from exhaustion by hunting, as well as by lightning, completely prevents the post-mortem rigidity of muscles, and the coagulation of the blood. But the observations of Gulliver† have proved that in animals killed by hunting and by fighting, the rigor mortis is greatly hastened, and that the blood does coagulate. He found that deer, foxes, and hares became quickly stiff after being hunted to death; and that game fowls, exhausted and worried to death by fighting, become quite stiff, and have the blood coagulated in their hearts within twenty-eight minutes after the last fatal wound. Rigor mortis, induced by exposure to heat or 'Heat rigor,' occurs in cold-blooded animals at 104°–109° F., in mammals at 118°–122° F., and in birds at 128° F. The immersion of Batrachian reptiles in water at a temperature of about 120° kills them instantly, all their muscles becoming immediately very stiff. The application of acids, even when very feeble or dilute, speedily causes 'acid rigor.' It may be said that all circumstances which tend to exhaust or depress the irritability of the muscles, such as death by slow and wasting disease, violent muscular exertion immediately before death, or powerful electrical shocks passed through the motor nerves, induce the early appearance and speedy departure of this state—putrefaction subsequently appearing and progressing rapidly. On the other hand, when the general energy has been retained up to a short period before death, as in persons who die from an accidental cause, or in animals the irritability of whose muscles has been augmented by cold, cadaveric rigidity sets in late and lasts long, and putrefaction also appears late and progresses slowly. Muscles deprived of blood by the ligature of their arteries, or brought into contact with distilled water, ammonia, dilute acids, alkaline salts, metallic salts, alcohol, or chloroform (all of which produce coagulation of the myosin, whilst some of them act on the other albuminous constituents of muscle), pass into a state closely analogous to, if not identical with Rigor mortis; and within certain limits their powers can be restored by the readmission of a current of duly oxygenated or arterial blood. The contractile force exerted in Rigor mortis, according to Hermann and Walker‡ is generally less than, though sometimes fully equal to, or even greater than that which the muscle can exert on strong electrical excitation.—The condition of the muscles in post-mortem rigidity is in many respects different from that of the contraction

* "Journ. of Anat. and Phys." 1874, p. 213.
† "Edinb. Med. and Surg. Journ.," Oct. 1848.
‡ Pflüger's "Archiv," Band iv. 1871, p. 182.

which occurs during life. In the former the shortening is persistent and uniform, the elasticity of the tissue is increased;* and when it is induced by Heat, a distinct diminution in the bulk of the muscle occurs; it feels firm and hard, and there are no signs of electrical disturbance; it cannot be excited to contract by the application of any stimulus. In the latter, on the contrary, the contraction is intermittent, and there is, as we have seen, a diminution in the amount of the elasticity and of firmness, and evidence of a change in the state of electrical tension (negative variation).—In Rigor mortis the muscles generally have an acid reaction, owing to the presence of sarco-lactic and glycerin-phosphoric acids; but this is not always the case, and the two conditions are therefore independent of each other.† According to Ranke‡ and Hermann, living muscle absorbs far more oxygen than dead; as is shown in the following table:—

Temperature.	*Excess of oxygen absorbed by living over dead muscle.*
0°—2° C.	24·73 vol. per cent.
7°—9° C.	14·72 „ „
15°—20° (Hermann's Experiment)	3·61 „ „
45°—55° C.	2·01 „ „

The absorption here indicated is clearly of a physiological nature, since it steadily diminishes with increasing elevation of temperature, which hastens the death of the muscle, and would prove favourable to any purely chemical changes.

637. It was formerly customary to divide the Muscles into two groups, termed the "voluntary" and "involuntary," coresponding to the "striated" and "non-striated" tissue respectively, but there are various circumstances which show that this system of classification cannot be consistently maintained. It is quite true that all the Muscles of Organic Life may be truly styled 'involuntary;' for although they are capable of being influenced by emotional and ideational states of mind, yet the Will cannot exert any direct influence upon them, only affecting them indirectly by its power of determining these states. But over those Muscles, also ministering to the organic functions, and doing so in obedience to impulses purely automatic, which are called into action by the Cranio-Spinal nerves, the Will, as we have seen, exerts some power; and such, therefore, cannot be properly regarded as involuntary, since the Will can influence their state; whilst they are far from being truly voluntary, since the Will cannot control their tendency to automatic action beyond a certain limited amount (§ 271). On the other hand, every one of the muscles usually styled voluntary, because ordinarily called into action by the Will, is liable to be thrown into action involuntarily; either by an Excito-motor stimulus, as in tetanic convulsions, or by Consensual action, as in tickling, or Emotionally, as in laughter or rage, or simply Ideationally, as in somnambulism and analogous states. Hence although there are certain groups of muscles which are more frequently acted on by the Will than by any other impulse, and certain others which are more frequently played on by the Emotions, and so on, it becomes obvious that every muscle called into contraction by the Cranio-Spinal nervous system is capable of receiving its stimulus to movement from *any* of these sources; the nerve-force transmitted along the motor-fibres being issued either from the Spinal Cord, from the Sensory Ganglia, or from the Cerebrum, as the case may be, but being in its nature and effects the same in every instance.

* There seems to be some difference of opinion on this point, Hermann and Walker (Pflüger's "Archiv," 1871, Band iv. p. 182) maintaining that muscles in Rigor mortis possess a greater extensibility than contracted muscles. † Wundt, "Physiologie des Menschen.," 1873, p. 476.

‡ "Die Lebensbedingungen der Nerven," 1868, p. 33.

638. The grouping or combination of muscular actions, which takes place in almost every movement of one part of the body upon another, must be attributed, not to any peculiar sympathy among the Muscles themselves, but to the mode in which they are acted on by the Nervous Centres. This is most obviously the case with regard to those of the primarily-automatic class; but it can scarcely be doubtful as to those of the secondarily-automatic kind (§ 501), such as walking, which, though at first directed by the Will, come by habit to be performed under conditions essentially the same with the preceding; and when it is borne in mind that even in voluntary movements the Will cannot single out any one muscle from the group with which it usually co-operates, so as to throw this into separate contraction, but is limited to determining the result, it seems pretty obvious that even here the grouping is effected by the endowments of those Automatic centres from which all the motor impulses immediately proceed to the muscles, and not by Cerebral agency. In fact, the whole process by which we acquire the power of adapting our muscular actions to the performance of some new kind of movement—as in the case of an infant learning to walk, a child learning to write, an artizan learning some occupation which requires nice manipulation, a musical performer learning a new instrument, and so on—is found, when attentively studied, to indicate that the Will is far from having that direct and immediate control over the contractions of the Muscles, which it is commonly reputed to possess; and that the operation really consists in the gradual establishment of a new grouping of the separate actions, in virtue of which the stimulus of a Volitional determination, acting under the guidance of the muscular sensations (§ 641), henceforth calls into contraction the group of muscles whose agency is competent to carry that determination into effect. For however amenable any set of muscles (as those of the arm and hand) may have become to the direction of the Will, in any operations which they have been previously accustomed to perform, it is only after considerable practice that they can be trained to any method of combined action which is entirely new to them; and even if we attempt to bring our anatomical knowledge into use for such a purpose, by mentally fixing upon certain muscles whose action we wish to intensify and to associate with those of others, we find that such a method of proceeding affords no assistance whatever, but rather tends to impede our progress, by drawing off the attention from the 'guiding sensations' (visual, muscular, &c.), which are the only regulators that can be depended upon for determining the due performance of the volitional mandate. —Hence we are led by these considerations, as by those stated in the preceding paragraph, to the conclusion, that the agency which directly affects the muscles is of the same kind, and that it operates under the same instrumental conditions, whatever be the primary source of the motor power. And in watching the gradual acquirement of the capacity for different kinds of movement, during the periods of Infancy and Childhood in the Human subject, we find everything to confirm this conclusion. For it becomes obvious that the acquirement of voluntary power over the movements of the *limbs* is just as gradual as it is over the direction of the *thoughts;* all the activity of the *body*, as well as of the *mind*, being in the first instance automatic; and the Will progressively extending its domination over the former, as over the latter, until it brings under its control all those muscular movements which are not immediately required for the conservation of the body, and our will turns them to its own uses.*

* The aptitude which is acquired by practice, for the performance of certain actions that were at first accomplished with difficulty, seems to result as much from a structural change

2. *Of the Symmetry and Harmony of Muscular Movements.*

639. It might have been not unreasonably supposed, *d priori*, that those muscles would have been most readily put to simultaneous contraction which correspond to each other on the two sides of the body; in other words, that *symmetrical* movements would be those most readily performed. Such, however, is by no means the case; for in many of our most familiar actions we consentaneously exert different muscles on the two sides of the body. This is nowhere more clearly shown than in the various movements that are required for the performance of the different acts of locomotion, and which may here be briefly noticed. In order to maintain the body in the erect posture, simple as the effort appears, the concurrent action of many muscles is required, as is clearly shown not only by the numerous and futile trials made by children before the power of balancing is acquired, but by the impossibility of placing a dead body in this position without support. In *standing*, the legs are more or less extended; and the weight of the trunk is transmitted through the femora and the tibiæ and fibulæ to the astragali. These, with the other tarsal and metatarsal bones, form an elastic arch on either side, which, whilst allowing the great superincumbent pressure to be borne with ease, enables each foot to accommodate itself to irregularities of the surface of the ground, and at the same time breaks the shock or jar which would otherwise be experienced in the various movements of walking, running, or leaping. The centre of gravity of the whole body lies, according to Weber, in the promontory of the sacrum; but, according to Meyer, in the canal of the second sacral vertebra. As long as a perpendicular line drawn from this point to the earth drops within the basis formed by the feet, the erect posture can be maintained with comparative ease; if it drop outside that basis, the subject must inevitably fall. The chief muscles called into play in the standing position are those which keep the head vertical on the spinal column, as the recti, obliqui, sternomastoids, splenii, complexus, &c., the extensors of the spine, as the erectores spinæ and their prolongations, and the extensors of the thigh and leg; but the opposite muscles are, as a sailor would express it, 'taut,' and ready to contract instantaneously and unconsciously on the slightest indication of loss of equilibrium.

640. *Walking.*—In this movement the body, supported in a nearly vertical position, alternately rests on the right and left leg; the limb upon which it does not rest swinging forward, like a pendulum, in a remarkably regular manner, just sufficiently bent to avoid contact with the ground. This is not effected, however, quite apart from muscular action, since, as M. Duchenne has shown, certain muscular paralyses (of flexor muscles) prevent the oscillation from occurring.* If we examine the successive movements which occur in making two steps, it will be found that if the subject be standing firmly with the left leg in advance, the first act consists in raising the heel of the

which the continual repetition of them occasions in the Muscle, as in the habit which the Nervous system acquires of exciting the movement. Thus almost every person learning to play on a musical instrument, finds a difficulty in causing the two shorter fingers to move independently of each other and of the rest; this is particularly the case in regard to the ring-finger. Any one may satisfy himself of the difficulty, by laying the palm of the hand flat on a table, and raising one finger after the other, when it will be found that the ring-finger can scarcely be lifted without disturbing the rest,—evidently from the difficulty of detaching the action of the portion of the *extensor communis digitorum*, by which the movement is produced, from that of the remainder of the muscle. Yet to the practised musician, the command of the Will over all the fingers becomes nearly alike; and it can scarcely be doubted that some change in the structure of the muscle, or a new development of its nerve-fibres takes place, which favours the isolated operation of its several divisions.

* Duchenne (de Boulogne), "Physiologie des Mouvements," Paris, 1867, p. 386.

right foot, which is accomplished by the gastrocnemius and soleus muscles; and the weight of the whole body thus raised is by the simultaneous contraction of the psoas and iliacus muscles of the left leg thrown over to the left side, resting for an instant upon the left foot. At this period all the extensors of the left leg, the glutæi, the quadriceps extensor femoris, the tibialis anticus, &c., are powerfully contracted. The right leg, the toe of which is the last part which touches the ground, now swings forward, the knee and hip joints being just sufficiently bent to enable the foot to clear accidental irregularities of the surface. Lastly, the right heel is planted on the ground in front, and is immediately followed by the whole surface of the foot; but coincidently with this occur the elevation of the left heel and the throwing over of the weight of the trunk to the right side, which is followed by the swinging forward and implantation of the left foot, and so on alternately. The weight of the legs in the act of swinging forward has been shown by Weber to be materially diminished by the pressure exerted by the atmosphere in retaining the head of the femur in the acetabulum. The ordinary rate of movement in walking for each person is to an important extent regulated by the length of the leg, and the consequent duration of its pendulum-like oscillation. Various compensatory movements in walking occur in order to maintain the equipoise of the body; amongst the most important of these are the movements of the arms, for whilst the right leg is swinging forward, the twisting of the trunk which occurs at this period would bring the right shoulder forwards, but the right arm at this moment sways backwards and the left forwards, and by thus generating a force in the opposite direction neutralizes this tendency. A corresponding compensation takes place when the left leg swings forward, and this is effected by a good walker without any sensible lateral twisting of the trunk.* The whole body rises and falls to a small amount ($1\frac{1}{4}$ inch) in walking, &c. The trajectory of any fixed point of the body, as the pubis, may, according to the formula of M. Carlet, be inscribed in a hollow half cylinder with its concave portion upwards, at the base of which lie the minima, and on the sides of which the maxima terminate tangentially. M. Carlet,† who has lately bestowed much attention on the movements of locomotion in man, divides each step into two parts—one, during which both feet are in contact with the ground (*temps du double appui*), and the other when the body is supported by one foot alone (*temps de l'appui unilatéral*). A. *Period of Double Contact.*—1. At the beginning of the period of double contact, when the foot in front only touches the ground with the heel, the posterior leg is stretched, and rests only on the extremities of the metatarsal bones and the phalanges. The knee of the front leg is extended or slightly flexed. The bicotyloidean axis is oblique, from before backwards, and from above downwards. The trunk descends at the same time that its lateral and forward inclination diminishes. The pubis is turned towards the side of the posterior leg. 2. In the middle of the period of double contact, that is to say when the front foot begins to touch the ground along its whole length, the posterior leg only touches it with its phalanges. The knee of the fore leg is rather more bent. The position of the bicotyloidean axis is the same as before. The trunk has gained its lowest position. The pubis is situated above the axis of the path to be pursued. 3. At the end of the period of double contact, that is when the posterior leg only touches the ground by

* See Bishop in "Cyclop. of Anat. and Phys.," vol. iii. p. 460.

† Carlet, 'Essais expérimentals sur la Locomotion,' in the "Annales des Sci. Nat.," 1872. The reader may also refer to Marey's 'Animal Mechanism,' vol. xi. of the "International Scientific Series," and to Pettigrew's 'Animal Locomotion,' vol. vii. of the same series.

the ends of its phalanges, the front leg has begun to extend the knee-joint. The bicotyloidean line is oblique as before. The trunk begins to be raised at the same time that it inclines forwards and to the side. The pubis is directed obliquely towards the side of the front leg. B. *Period of Single or Unilateral Contact.*—1. At the beginning of this period, that is when the posterior foot is about to quit the ground, and the front foot is planted flat, the supporting leg continues to open or extend the knee-joint, whilst the opposite one begins to be flexed. The bicotyloidean axis is oblique, but from before backwards only, being otherwise horizontal; the trunk begins to rise at the same time that it inclines forwards and to the side. The pubis is directed obliquely outwards, towards the side of the leg in front. 2. In the middle of the period of unilateral support, that is when the heel of the supporting leg quits the ground, it extends the articulation of the knee to the utmost. In the leg that is suspended in the air, on the contrary, the knee is flexed to its maximum amount. The bicotyloidean axis is always oblique, but from above downwards only. It lies in a vertical plane, and its lower extremity corresponds to the supporting limb; the trunk has reached its greatest elevation, and at the same time its inclination forwards and to the side is at its maximum. The pubis is at its maximum of obliquity as regards the path pursued on the side of the supporting leg. 3. At the close of the period of unilateral support—that is, when the supporting leg touches the ground only by its metatarso-phalangeal portion, and the free leg has passed the middle of its period of oscillation, the ankle-joint of the supporting leg extends or opens whilst that of the knee remains at its maximum of extension. The bicotyloidean axis becomes again oblique from before backwards, and from above downwards; but its obliquity is now in the opposite direction, and the limb which was in front and above in the period of double contact is now behind and below. The trunk descends at the same time that its forward and lateral inclination diminishes. The pubis approximates the axis of the path. If the length of the steps increases, their duration in *general* diminishes, whilst the falling of the trunk and its inclination always augment. The number of steps in a given time, or the pace of walking, is partly dependent upon the length of the legs, and partly upon direct muscular effort: the longer the leg, the slower will be the oscillation; but by planting the foot on the ground when it has only passed through one-half of its natural oscillation, the succession of steps, and consequently the rapidity of progress, can be materially increased without much effort. In very quick walking almost every muscle in the body is brought into play; the trunk is considerably inclined forwards, partly for the purpose of resisting and compensating for atmospheric pressure, but chiefly to enable the hip-joints to be carried low, thus increasing the extent of ground which can be covered by each step, whilst at the same time the number of steps is greatly increased by muscular effort; the period during which both feet are resting on the ground together being considerably shortened. In an experiment made by Mr. Vasey, the length of whose leg was thirty-four inches, in walking at the rate of four miles an hour, 2,000 steps were made every fifteen minutes; the length of each step must therefore have been 2·64 feet, and the time of each step 0·45 second. M. Carlet has shown that the muscular effort in walking, as indicated by the backward push, supposing the weight of the individual to be about 150 pounds, does not surpass 45 pounds additional, though it is much greater in leaping and running.—Quick walking passes by insensible gradations into *running*, the period in which the body rests upon both feet becoming shorter and shorter, until at length there is a period between successive steps during which the body moves forward unsupported

by either foot. According to Weber, the vertical undulations of the trunk in running vary from 3–4ths to 4–5ths of an inch, the duration of the step from 1–4th to 1–5th of a second, of which time the body swings unsupported in the air 1–10th of a second, the time of descent being 1–15th of a second.—In *leaping*, the extensor muscles are brought into extremely vigorous action, and the act may be accomplished either by the alternative or the simultaneous action of the legs, as seen in the "hop, step, and jump" of children. The essential difference in leaping and running is, that in leaping the body is raised so high from the ground and for so long a period that the leg or legs have time to complete their full arc of oscillation, and consequently cover the utmost space of ground possible. The extent of the leap is of course dependent upon the muscular energy of the individual.*

641. Now it is plain that the grouping of the muscular movements in these different instances arises out of its *felt* conformity to the end in view, and that it is regulated by the guiding sensations which indicate to us the progression and balance of the body. The infant, in learning to walk, is prompted by an instinctive tendency to put one foot before the other, as may be noticed at a very early period, when it is first held so as to feel the ground with its feet; and in attempting to balance itself when first left to stand alone, it moves its arms with a like intuitive impulse, not based upon experience. All that experience does, in either case, is to give that precise adjustment to the muscular action which makes it perfectly conformable to the indications afforded by the muscular sensations. Thus, if we advance each arm with its corresponding leg, we feel that the balance of the body is not nearly as readily maintained as it is when we advance the arm with the leg of the opposite side; and thus, without any design or voluntary determination on our parts, the former comes to be our settled habit of action. This kind of adjustment, as in the case before us, is by no means limited to the muscles of the limbs; for there is scarcely any muscle of the trunk or head that is not exerted with some degree of consentaneous energy, however unconsciously to ourselves, in the act of walking. The difficulty which would attend the voluntary harmonization of all these separate actions is remarkably evinced by the fact, that no mechanist, however ingenious, has ever succeeded in constructing an automaton that should *walk* like Man; the alternate shifting of the centre of gravity from one side to the other, upon so small a base as the human foot affords, simultaneously with the movement in advance, constituting the great difficulty of biped progression. But all this adjustment is effected in our own organism *for* us, rather than *by* us; the act of harmonization, when once fully mastered, being attended with no effort to ourselves; but the whole series of complex movements being performed in obedience to the simple determination *to walk*, under the automatic guidance of the senses, which instantly reveal to us any imperfection in the performance.—The same view extends itself readily to other combinations of dissimilar and non-symmetrical movements, which are less *natural* to Man, but which may be readily acquired *artificially* if they all harmonize in a common purpose and are under the guidance of the same set of sensations. Thus, the performer on the Organ uses the several fingers of his two hands to execute as many different movements (in very different positions, it may be) on the 'manual' keys: one of his feet may be on the 'swell' pedal, and the other

* The subject of the locomotion of Man has been particularly investigated by the Profrs. Weber, whose work entitled "Mechanik der menschlich. Gehwerkzeuge" (Göttingen, 1836) has been translated in Jourdan's "Encyclopédie Anatomique," tom. ii. See also the Art. 'Motion' by Mr. J. Bishop, in "Cyclop. of Anat. and Physiol.," vol. iii.

may be engaged in playing on the 'pedal' keys; but all these diverse actions are harmonized by their relation to the same set of auditory sensations; and if the result be not that which the performer anticipated, an immediate correction is made. The preferential use of the right arm and leg is not easily explicable. Dr. Pye-Smith* refers it to the principle of the "survival of the fittest," contending that in warfare those who advanced the right side would in the long run be exposed to less risk of fatal wounds. Dr. Ogle,† however, points out that the right extremities are used preferentially by other animals, as the monkey and parrot, and refers it to the fact that the left hemisphere receives a freer supply of blood than the right. It may to some extent proceed from imitation, and to some extent also be the result of education.

642. It would be easy to multiply instances of the same kind, all illustrative of the general principle, that the facility with which we voluntarily combine different movements is chiefly determined, not by their *symmetrical* character, but by their *conformableness to a common end*, and by the *harmony of their guiding sensations* with reference to that end;‡ but it will be desirable to dwell particularly on the *Movements of the Eye*, as presenting certain points of peculiar interest, some of which have an important bearing on Surgical practice.—It will be recollected that in the Human Orbit, six muscles for the movements of the eyeball are found; the four Recti, and the two Oblique muscles. The precise actions of these are not easily established by experiment on the lower animals; for in all those which ordinarily maintain the horizontal position, there is an additional muscle, termed the *retractor*, which embraces the whole posterior portion of the globe, and passes backwards to be attached to the bottom of the orbit.§ If the origin and insertion of the four *Recti* muscles be examined, however, no doubt can remain that each of them, acting singly, is capable of causing the globe to revolve in its own direction—the superior rectus causing it to roll towards the nose—and so on. A very easy and direct application of the laws of mechanics will further make it evident to us, that the combined action of any two of the Recti muscles must cause the pupil to turn in a direction intermediate between the lines of their single action; and that *any* intermediate position may thus be given to the eyeball by these muscles alone. In two directions, however, their combined action is supplemented by the oblique muscles. The superior oblique rotates the eye downwards and outwards; the inferior oblique upwards and outwards. Another important operation of the oblique muscles is to maintain the

* "Guy's Hosp. Rep.," 1871.

† 'Rep. of Med.-Chir. Soc.,' "Lancet," 1871, p. 449. See also, for scattered Notes and Observations on this subject, "Lancet," 1860, vol. i. pp. 526, 557, 660; 1871, vol. i. p. 495; vol. ii. pp. 49 and 111; Buchanan, 'Theory of the Right Hand,' "Edinburgh Med. Journ.," 1863; and Pamphlet, Glasgow, 1862. Poncet, "Gaz. Hebdom.," 1875, No. 36, finds that in right-handed persons the right, in left-handed persons the left, bones exceed those of the opposite side in weight by about 17 grammes = 262·48 grains, or nearly half an ounce.

‡ Two simple examples, however, may be cited, of the difficulty which attends the simultaneous performance of movements that are not harmonious. If we attempt to elevate one eyelid whilst we are depressing the other, we find that a considerable effort is required to accomplish the action, although the elevation or depressing of both eyelids together is performed with so little effort that we are scarcely conscious of it; and the difficulty is increased if we half shut both eyes, and then try to close one and to open the other. So if we try to move our two hands as if they were *simultaneously* winding cord *in opposite directions* upon two reels placed in front of us, we shall find ourselves unable to do so without a constant exercise of the attention, and even then but slowly and with difficulty; although the very same movements may be *separately* performed, or both hands may be made thus to move *in the same direction* with the greatest facility.

§ See Alfred v. Gräfe, "Klinische Analyse der Motilitäts-störungen des Auges," and v. Gräfe's "Archiv f. Ophthalmologie," Band i.-iii.

parallelism of the vertical meridians of the two eyes in certain movements, for it is found that whilst the external and internal recti merely turn the eyes outwards and inwards, without deflecting the vertical meridian, the superior and inferior recti, in consequence of the obliquity of their muscle planes, not only rotate the eye respectively upwards and downwards, but deflect the upper extremity of the vertical meridian, the former inwards, the latter outwards. But the oblique muscles also deflect the vertical meridian, the superior turning the upper extremity of the vertical meridian inwards, the inferior outwards, and therefore by co-operating with the recti, are able to preserve the parallelism of the vertical meridians of the two eyes, as shown in the following table:

Movement	Is effected by the
Upwards	Superior rectus, aided by the inferior oblique.
Downwards	Inferior rectus, aided by the superior oblique.
Inwards	Internal rectus.
Outwards	External rectus.
Upwards and inwards	Superior and internal recti muscles, aided by the inferior oblique.
Upwards and outwards	Superior and external recti muscles, aided by the inferior oblique.
Downwards and inwards	Inferior and internal recti muscles, aided by the superior oblique.
Downwards and outwards	Inferior and external recti, aided by the superior oblique.

643. On studying the voluntary movements of the Eyeballs we are led to perceive that they are not so much *symmetrical* as *harmonious*—that is to say, the corresponding muscles on the two sides are rarely in action at once; whilst such a harmony or *consent* exists between the actions of the muscles of the two orbits, that they work to one common purpose—namely, the direction of both eyes towards the required object. They may be arranged under two groups; the first comprising those which are alike harmonious and symmetrical; the second including those which are harmonious but not symmetrical. To the *first* group belong the following:—1. *Both* eyeballs are *elevated* by the contraction of the two Superior Recti.—2. *Both* eyeballs are *depressed* by the conjoint action of the Inferior Recti muscles.—3. *Both* are drawn directly *inwards*, or *inwards* and *downwards*, as when we look at an object placed on or near the nose: this movement is effected by the action of the Internal Recti of the two sides, with or without the Inferior Recti. It is evidently symmetrical, but might seem at first sight not to be harmonious, because the eyes do not move together towards one side or the other; it is, however, really harmonious, since it directs their axes towards the same point.*—Now it is to be observed, with regard to these movements, that we can never effect them in antagonism with each other, or with those of other muscles. We cannot, for example, raise one eye and depress the other; nor can we raise or depress one eye, when we adduct or abduct the other. The explanation of this will be found in the fact, that we can never, by so doing, direct the eyes to the same point.—The harmonious but unsymmetrical movements forming the *second* class, are those in which the Internal and External Recti of the two sides are made to act together, either alone, or in conjunction with the Superior and Inferior Recti.

* Some persons can effect this voluntarily to a greater extent than others; but even then they can only accomplish it by fixing the gaze upon some object situated between the eyes; and cannot call the adductor muscles into combined action in perfect darkness, or if the lids be closed. Even those who have the least power of effecting this extreme convergence, by at once directing the eyes towards a very near object, can accomplish it by looking at an object placed at a moderate distance, and gradually bringing this nearer to the nose, keeping the eyes steadily fixed upon it. The unwonted character of the movement is shown in this—that it can only be maintained, even for a short time, by a strong effort, producing a sense of fatigue.

They are as follows :—4. *One* eye is made to revolve directly *inwards* by the action of its Internal Rectus, whilst *the other* is turned *outwards* by the action of its External Rectus.—5. *One* eye is made to revolve *upwards* and *inwards*, by the conjoint action of the Superior and Internal Recti; *the other upwards* and *outwards*, by the conjoint action of the Superior and External Recti.—6. *One* eye is made to revolve *downwards* and *inwards*, by the conjoint action of the Inferior and Internal Recti; *the other*, *downwards* and *outwards*, by the conjoint action of the Inferior and External Recti.—In these movements, *two different* muscles, the External and Internal Recti, are called into action on the two sides, with or without the superior and inferior Recti; but they are so employed for the purpose of directing the axes of the eyes towards *the same* point; and although, as just noticed, we can put the two Internal Recti in action together, we cannot voluntarily cause the two External Recti to contract together, it not being possible that any object should be in such a position as to require this action for the direction of the axes of the eyes towards it.

644. The greater number of the foregoing movements may be performed unconsciously to ourselves, in obedience to a Voluntary determination to keep the direction of the eyes fixed, instead of to give motion to the eyeballs. Thus, if we gaze steadily at an object in front of us, and then depress the head forwards on its transverse axis, the eyeballs roll upwards upon their transverse axes (1) by the action of the Superior Recti, without our being aware of it; so if, whilst still maintaining the same fixed gaze, we raise the head into the vertical position and then depress it backwards, the eyeballs are rolled downwards (2) by the action of the Inferior Recti; if, under the same conditions, the head be made to rotate on its vertical axis from side to side, the eyeballs will be made to roll on their vertical axes in the contrary directions by the External and Internal Recti (3) of the two sides respectively; so, by causing the head to move obliquely in the opposite directions, the reverse oblique movements (4 and 5) of the eyeballs are made to take place by the continued fixation of the vision upon the same object. To these we have to add one more action, which cannot be called forth in any other mode—namely, that rotation of the eyes upon their antero-posterior axes, which takes place probably by the instrumentality of the Oblique muscles, when we incline the head to one side or the other by rotating it upon its antero-posterior axis. In all these movements, as in the preceding, the Will directs the *result*; and there is no other difference between them, than that which arises out of our consciousness of a change in the one case, and our unconsciousness in the other. It may here be remarked that Prof. Helmholtz* has recently adopted the same view as that just expressed in regard to the nature of the volitional direction and the influence of the guiding sensations; in corroboration of which he further mentions the important fact ascertained by Donders and himself, that by the use of a prism before one eye, *both* eyes may be made to move *outwards*, or one up and the other down—still under the same fundamental law.—The truly involuntary movement of the eyeballs, however, are performed under very different conditions; there being here no purposive direction or fixation of the gaze; and the muscular contractions not being determined by visual sensations, but being called forth by nerve force excited in some remote part. Of this we have an example in the normal revolution of both eyes upwards and inwards, which takes place in the acts of coughing, sneezing, winking, &c.; but far more remarkable illustrations are presented in those abnormal movements

* In his Croonian Lecture, "Proceedings of the Royal Society," April 14, 1864, p. 193.

of the eyeballs occurring in Convulsive diseases, in which there is neither harmony nor symmetry.

645. It has been stated to be a condition of single and distinct vision, that the *usual* axes of the eyes should be directed towards the object, in order that its picture should be thrown upon the parts of the two retinæ which are *accustomed* to act together (§ 566) ; but as this cannot take place without the guidance of visual sensations, the movements of the eyeballs are wanting in harmony whenever the visual power has been deficient from birth. This is most remarkably the case, where the deficiency has been so complete that not even light can be distinguished; but the movements are frequently very far from being harmonious, in cases of congenital cataract, where a considerable amount of light is evidently admitted, but where no distinct image can be formed ; and in such cases, the movements are most harmonious where the object is bright or luminous, and more vivid impressions are therefore made upon the retinæ. It is no objection to this doctrine to say, that persons who have *become* blind may still move their eyes in a harmonious manner; since the habit of the association of particular movements having been once acquired, the guidance of the muscles may be affected by sensations derived from themselves, in the manner in which it takes place in the laryngeal movements of the deaf and dumb; and, as a matter of fact, a want of consent may often be observed where the blindness is total. The peculiar 'vacant' appearance, which may be noticed in the countenances of persons completely deprived of sight by amaurotic or other affections, which do not alter the external aspect of the eyes, seems to result from this—that their axes are *parallel*, as if the individual were looking into distant space, instead of presenting that slight convergence which must always exist between them, when the eyes are fixed upon a definite object. This convergence, which is of course regulated by the Internal Recti, varies in degree according to the distance of the object; and it is astonishing how minute an alteration in the axes of the eyes becomes perceptible to a person observing them. For instance, A sees the eyes of B directed towards his face, but he perceives that B is *not looking* at him ; he knows this by a sort of intuitive interpretation of the fact, that his face is not the point of convergence of B's eyes. But if B, who might have been previously looking at something nearer or more remote than A's face, fix his gaze upon the latter, so that the degree of the convergence of the axes is altered, without the general direction of the eyes being in the least affected, the change is at once perceived by the person so regarded; and the *eyes* of the two then *meet*.—It is an interesting confirmation of the principles here advocated, that when binocular vision cannot be obtained by directing the true axes of the eyes towards the object, as happens when an opaque spot exists upon the centre of the cornea, or an artificial pupil has been formed at the margin of the iris, there is an automatic tendency to the neutralization of the mischief, by such an action of the muscles as shall turn the *virtual* axis of the affected eye (that is, the axis in which the rays most directly enter the globe) towards the object, thus producing Strabismus, but *not* Double Vision.

3. *Energy and Rapidity of Muscular Contraction.*

646. The energy of Muscular contraction is of course to be most remarkably observed in those instances in which the continual exercise of particular parts has occasioned an increased determination of blood towards them, and in consequence a permanent increase of their bulk (§ 330). This has been the case, for example, with persons who have gained their livelihood by exhibiting feats of strength. Much will, of course, depend on the mechanically-advan-

tageous application of muscular power; and in this manner effects may be produced, even by persons of ordinary strength, which would not have been thought credible. In lifting a heavy weight in each hand, for example, a person who keeps his back perfectly rigid, so as to throw the pressure vertically upon the pelvis, and only uses the powerful extensors of the thigh and calf, by straightening the knees (previously somewhat flexed), and bringing the leg to a right angle with the foot, will have a great advantage over one who uses his lumbar muscles for the purpose. A still greater advantage will be gained by throwing the weight more directly upon the loins, by means of a sort of girdle, shaped so as to rest upon the top of the sacrum and the ridges of the ilia; and by pressing with the hand upon a frame, so arranged as to bring the muscles of the arms to the assistance of those of the legs: in this manner, a single man of ordinary strength may raise a weight of 2000 lbs.; whilst few who are accustomed to such exertions, can lift more than 300 lbs. in the ordinary mode. A man of great natural strength, however, has been known to lift 800 lbs. with his hands: and the same individual performed several other curious feats of strength, which seem deserving of being here noticed. "1. By the strength of his fingers, he rolled up a very large and strong pewter dish. 2. He broke several short and strong pieces of tobacco-pipe with the force of his middle finger, having laid them on the first and third finger. 3. Having thrust in under his garter the bowl of a strong tobacco-pipe, his legs being bent, he broke it to pieces by the tendons of his hams, without altering the bending of the knee. 4. He broke such another bowl between his first and second fingers, by pressing them together sideways. 5. He lifted a table six feet long, which had half a hundred weight hanging at the end of it, with his teeth, and held it in that position for a considerable time. It is true, the feet of the table rested against his knees; but as the length of the table was much greater than its height, that performance required a great strength to be exerted by the muscles of his loins, neck, and jaws. 6. He took an iron kitchen poker, about a yard long, and three inches in circumference, and holding it in his right hand, he struck it on his bare left arm between the elbow and the wrist, till he bent the poker nearly to a right angle. 7. He took such another poker, and, holding the ends of it in his hands, and the middle of it against the back of his neck, he brought both ends of it together before him; and, what was yet more difficult, he pulled it straight again."* Haller mentions an instance of a man, who could raise a weight of 300 lbs., by the action of the elevator muscles of his jaw: and that of a slender girl, affected with tetanic spasm, in whom the extensor muscles of the back, in the state of chronic contraction or opisthotonos, resisted a weight of 800 lbs. laid on the abdomen with the absurd intention of straightening the body.

647. *Absolute Force of Muscle.*—The mechanical power exerted by muscle in contraction may be calculated as in any mechanical machine, by multiplying the weight lifted by the height to which it is raised. Weber obtained the following values for the muscles of a frog;—

	Weight lifted in Grammes.		Height in Mm.		Mechanical effect in Grammillimetres.
a	5		27·6		138
b	15	× by	25·1	=	376
c	25		11·45		286
d	35		6·3		220

That is to say, that 138 grammillimetres are equal to 5 grammes raised 27·6 mm. or to 27·6 grammes raised 5 mm. It will be seen from the table that the mechanical effect increases to a certain point with the weighting, and then

* Desagulier's "Philosophy," vol. ii.

gradually diminishes: it was found that different muscles had their maximum weightings.—The power of the muscles appears to vary in different animals, being greatest in proportion to their size in Insects.* The relation of the muscles of the same animal to one another is very simple, the weight which can be raised, as Professor Haughton† states, being proportional to the area of the cross section of each muscle, and may even be estimated by the cross section of the tendon that conveys its influence to a distant point; whilst it is obvious that a given weight can be raised higher in proportion to the length of the muscle. The most natural measure of the maximum of force which is exerted when the muscle is in its highest state of excitability is the amount of work it can accomplish under the influence of the strongest stimulus. But this, as is shown above, is found to vary with the degree of weighting; and it is, therefore, advantageous to adopt another measure to which the term "absolute muscle-force" may be applied.‡ This is represented by the weight, which is exactly equivalent to the contractile power of the muscle when stimulated to its utmost, or, in other words, which the muscle, when most strongly stimulated, is just incapable of raising. The absolute muscle-force for the square centimetre of the muscles of the frog was estimated by Weber at 692 grammes. Rosenthal§ gives a higher number for the muscles of the same animal, estimating it at from 2300 to 3000 grammes per square centimetre of cross section for the adductor magnus and semi-membranosus, and from 1000 to 1200 grammes for the gastrocnemius; whilst for the square centimetre of the muscle of man, Henke and Knorz have estimated it at from 6000 to 8000 grammes; and Koster‖ at about 10,000 grammes per square centimetre for the muscles of the leg, and 7400 for those of the arm. Haughton's estimate¶ agrees very closely with those of Henke and Knorz, since he considers the absolute muscle-force of the muscles of the human arm to be 94·7 lbs., of the leg to be 110·4 lbs., and of the abdomen to be 107 lbs. for the square inch of sectional area, which reduced to French measure** would amount to about 7700 grammes for the square centimetre. Mr. H. F. Baxter†† found from his experiments that one grain of frog's muscle is on the average capable of raising a weight of 608 grains through a space of 1-63rd of an inch, though considerable differences exist in regard to sex, age, and general condition of the animal. Thus he found that whilst one grain of the muscle of male frogs could raise 656 grains, one grain of the muscle of female frogs could only raise 579 grains. Again in March and April one grain of frog's muscle raised 445 grains $\frac{1}{63}$ of an inch high, in June and July 608 grains.‡‡ This agrees with the observation of Schmulewitsch,§§ that within certain limits the higher the temperature of muscle, the more work is it able to perform with equal weighting and stimulus. Fick‖‖ finds the power possessed by one grain of frog's muscle to be 5000 millimetre-grammes for one single contraction. Haughton¶¶ estimates that one ounce of the human heart

* See Plateau, "Révue Suisse," t. xxv. 1866, p. 87, who states that the Donacia nymphæa can overcome a resistance equal to forty-two times its own weight.

† "Proceedings of Royal Society," 1867, No. 94.

‡ See Hermann, "Grundriss der Physiologie," 1867, p. 238.

§ "Comptes Rendus," tom. lxiv. p. 1143. ‖ "Archief Nederland," Band ii. No. 2.

¶ "Proceedings of the Royal Society," 1867, No. 94.

** Taking the square inch at 6·45 square centimetres, and the pound avoirdupois at 453·59 grammes.

†† 'On Muscular Power,' in the "Edin. New Phil. Journ.," vol. xviii. p. 194.

‡‡ "Archives of Medicine," vol. iv. pp. 298 and 326.

§§ "Centralblatt," 1867, No. 6; and "Medicin. Jahrb.," Band i.

‖‖ Virchow's "Jahresb." for 1867, p. 80.

¶¶ "Outlines of a New Theory of Muscular Action," Dublin, 1863.

will lift 20·576 lbs. through a height of one foot per minute, and that one lb. av. weight of human muscle is capable of lifting 1·56 ton through one foot before it is exhausted. Mr. Baxter's experiments also show the interesting circumstance that whilst there is a loss of weight in the animal during prolonged muscular contraction, there is an increase of weight in the individual muscles experimented on.—It is to be recollected, that the mechanical application of the power developed by muscular contraction to the movement of the body, is very commonly disadvantageous as regards *force:* being designed to cause the part moved to pass over a much greater *space* than that through which the muscle contracts. Thus the temporal muscle is attached to the lower jaw at about one-third of the distance between the condyle and the incisors; so that a shortening of the muscle to the amount of half an inch, will draw up the front of the jaw through an inch and a half; but a power of 900 lbs. applied to the muscle, would be required to raise 300 lbs. bearing on the incisors. In the case of the fore-arm and leg, the disproportion is much greater; the points of attachment of the muscles by which the knee and elbow-joints are flexed and extended, being much closer to the fulcrum, in comparison with the distance of the points on which the resistance bears. Professor Haughton has also shown that there is a loss in the force applied by the muscles of various animals in consequence of the friction of their tendons, which amounts in a man to 35 per cent., in the mastiff to 41 per cent., and in the kangaroo to 61 per cent. It may be instructive to append here the estimates made by different observers of the amount of work that a man weighing about 150 lbs. can with vigorous exertion accomplish in the course of a day of eight hours. The French assume as a work-unit the force that is requisite to raise one kilogramme (= 2·2 lbs.) one metre (= 39·37 in.) high in one second of time:—

Kind of labour.	Amount of work in foot-tons.	Authority.
Pedestrians	353	Haughton.
Pile-driving	312	Coulomb.
Pile-driving	352	Lamande.
Turning a winch	374	Coulomb.
Porters carrying goods and returning unloaded	325	„
Porters always loaded	303	„
Porters carrying wood upstairs and returning unloaded	381	„
Paviours at work	352	Haughton.
Prisoners at shot-drill	310	„

The mean of these estimates is 340·2 ft.-tons, or 762,048 ft.-pounds = 105,605 kilogrammetres, which closely accords with the estimate of Professor Donders.* In his Address at the Meeting of the British Association at Oxford, Professor Haughton estimated the daily external work of a working man at 353·74 foot-tons and adds 133 foot-tons for the work requisite to maintain the circulation and respiration. Ranke† gives the following table from Redtenbacher:—

The amount of work accomplished in eight hours by	Kilogr. in 8 hours.
1. Man, weighing on the average 70 kilog., working without machine	316,800
„ with a lever (Hebel)	158,400
„ with a windlass (Kurbel)	184,320
„ with a whinsey or gin	207,360
„ with a treadwheel	241,920
„ with an inclined plane, 24°	345,600
2. Horse, weighing on the average 280 kilog., working without a machine	2,102,400
„ with a gin	1,152,000

* See Dr. Moore's translation of his Paper in Humphry and Turner's "Journal of Anatomy," vol. i. 1867, p. 168.

† "Grundzüge der Physiologie," 1868.

The amount of work accomplished in eight hours by	Kilogr. in 8 hours.
3. Ox, weighing on the average 280 kilog., without machine	1,382,400
„ with a gin	1,123,200
4. Mule, weighing on the average 230 kilog., without machine	1,497,600
„ with gin	777,600
5. Ass, weighing on the average 168 kilog., without machine	864,000
„ with gin	316,800

Reducing these results to a general measure for a given weight, Ranke estimates that—

1 kilog. of human muscle works in 1 sec., without machine,					0·157 kilog.
„	ox	„	„	„	0·172 „
„	ass	„	„	„	0·178 „
„	mule	„	„	„	0·222 „
„	horse	„	„	„	0·261 „

He calculates eight hours' walking to be equivalent to 200,000 kilogr.

648. *Sources of Muscular Force.*—Muscle has been defined by an able chemist to be a machine by which heat is converted into mechanical force; and the results of numerous recent researches tend to show that the source of the primary heat is to be looked for in the oxidation of both the nitrogenous and of the non-nitrogenous constituents of the blood; the combination taking place partly within the bloodvessels, but chiefly in those portions of the blood which, escaping from the vessels, supply the tissue with the materials requisite for its nutrition. That nitrogenous substances are oxidized during muscular exertion is sufficiently proved by the necessity that exists for their free supply in groups of men, as navvies, prizefighters, &c., who have to maintain severe and protracted exertion, as well as by the fact ascertained by Parkes (§ 367) and Flint (§ 367) that a slight increase in the amount of the products of the disintegration of the nitrogenous constituents of the body does take place during exercise, becoming apparent by an increased elimination of nitrogen some hours after the exercise has been taken, whether the diet have contained a regulated amount of nitrogen, or has been wholly restricted to non-nitrogenous substances. That the force daily exerted by the muscles of a labouring man is, however, not exclusively derived from the combustion of the nitrogenous constituents of his muscles or of his blood, is proved by the circumstance that the elimination of urea, which may be regarded as the final product in the animal body of the decomposition of the albuminoid compounds, is not proportional to the amount of force expended;* and, secondly, by the fact that even allowing a margin for errors of calculation and experiment, the absolute quantity of nitrogen eliminated by the body represents an amount of albuminous material the combustion of which is insufficient to account for the muscular force that is generated with even moderate exertion. That the oxidation of the non-nitrogenous materials of the blood occurs during work, to furnish the heat which the muscles transform into mechanical force, is shown, first, by the greatly increased amount of carbonic acid contained in the venous blood of a contracting muscle, as compared with a muscle at rest (Sczelkow); secondly, by the increased elimination of carbonic acid and water that occurs during exercise (E. Smith, § 311); thirdly, by

* In his recent Memoir on the 'Source of Muscular Power' ("Journ. of Anat. and Physiol.," vol. xii. 1878, p. 141), Austin Flint states that in his experiments upon a man walking 317½ miles in five consecutive days, who at the beginning of the five days had no superfluous fat, the loss of weight was actually 3·45 lbs., while the total amount of nitrogen discharged from the body in the urine and fæces in excess of the nitrogen of the food taken for these five days, assuming that three parts of nitrogen represent 100 parts of muscular substance, as has been shown by analysis to be the fact, amounted to 3·037 lbs. of muscular substance. Hence he argues that in excessive muscular work a certain amount of muscular substance is consumed.

the fact that in some animals, as in bees (Verloren), as well as in man, (Fick, Parkes) a considerable amount of exertion can be temporarily undertaken on a diet containing little or no nitrogen, as sugar and fat, though it has been clearly shown that if the diet be exclusively confined to non-nitrogenous material, weakness and weariness soon supervene, quickly followed by complete muscular exhaustion (Hammond, Savory, Parkes). It may be remarked, also, that in those nations, and in those animals, that are well supplied with nitrogenous compounds in their food, a superior physical condition is produced, enabling them to maintain severe exertion for a longer period, and also to exert, when occasion may require, more vigorous effort for a shorter period, than those whose diet is of a poorer quality, or contains less nitrogen in an easily assimilable form. The precise seat of the oxidation cannot be held to be decisively ascertained, and some, but not very satisfactory evidence has been brought forward to show that it takes place within the vessels. The chemical facts connected with the contraction of muscle have been ingeniously woven by Hermann* into the following theory. He supposes that muscle contains a store of a complex nitrogenous material in a state of solution. It is unstable, and in the act of disintegration developes force. The products of its disintegration are, *inter alia*, carbonic acid, paralactic acid (possibly as Ranke believes, sugar and fat), and an albuminous compound which in the living muscle is gelatinous, but soon coagulates into a solid substance (Myosin). When at rest the disintegration proceeds slowly, but it is rendered more energetic by elevation of temperature within certain limits, and is induced instantly by certain "irritants." As the muscle substance is gradually consumed by exertion, it is requisite for the maintenance of its characteristic properties that a constant circulation of blood should take place through its vessels, by which means not only may oxygen and fresh supplies of nutritive material be brought to it, but the products of its disintegration, the presence of which seriously impairs its contractile powers, may be removed.† The power of the muscles appears to be capable of being increased by the passage of a continuous electrical current through the nerves supplying them.‡ Thus, Dr. Poore has shown that in a case where a man could hold his arm outstretched for six minutes, when the current was used he could go on for thirteen minutes. So also eight successive squeezes of the dynamometer without galvanism gave 388 lbs., and the same number with galvanism 477 lbs. Similar observations have been made by Heidenhain and Remak, who have termed such currents 'refreshing' or 'restorative.'

649. The rapidity of the changes of position of the component particles of muscular fibres, may, as Dr. Alison justly remarks,§ be estimated, though it can hardly be conceived, from various well-known facts. The pulsations of the heart can sometimes be distinctly numbered in children at more than 200

* "Grundriss der Physiologie," 1867, p. 226. See also Schenk, "Archiv f. Exper. Path.," 1874, Band ii. p. 21.

† The reader will find much interesting information on the several views of the origin of muscular force, with references to previous writers, in Playfair's "Essay on the Food of Man in Relation to his Useful Work," Edinb., 1865; Heaton's 'Essay on the Function of the Blood in Muscular Work,' "Phil. Mag," 1867; Donders, "On the Constituents of Food in their Relation to Muscular Work and Animal Heat," translated by Dr. Moore, Dublin, 1866; Parkes's 'Essays on the Elimination of Nitrogen by the Kidneys' ("Proceedings of the Royal Society," 1867, Nos. 89 and 94); "Proceed. Roy. Soc.," Lond., 1874, No. 150; Professor Haughton's "Address at the Meeting of the British Medical Association," 1868; and Austin Flint's 'Essay on the Source of Muscular Power,' in the "Journal of Anatomy and Physiology," vol. xii. 1878, p. 91.

‡ See the experiments of Dr. Poore, "Practitioner," January, 1873.

§ "Cyclopædia of Anatomy and Physiology," Art. 'Contractility.'

in the minute; and as each contraction of the ventricles occupies only half the time of the whole pulsation, it must be accomplished in 1-400th of a minute, or 3-20ths of a second. Again, it is certain that, by the movements of the tongue and other organs of speech, 1500 letters can be distinctly pronounced by some persons in a minute: every one of these must require a separate contraction of muscular fibres; and the production and cessation of each of the sounds implies that each separate contraction must be followed by a relaxation of equal length; each contraction, therefore, must have been effected in 1-3000th part of a minute, or in 1-50th of a second. Haller calculated that, in the limbs of a dog at full speed, muscular contractions must take place in less than 1-200th of a second, for many minutes at least in succession.—All these instances, however, are thrown into the shade by those which may be drawn from the class of Insects. The rapidity of the vibrations of the wings may be estimated from the musical tone which they produce; it being easily ascertained by experiments what number of vibrations are required to produce any note in the scale (§ 598). From these data, it appears to be the necessary result, that the wings of many Insects strike the air *many hundred* or even *many thousand* times in every *second*.—The minute precision with which the degree of muscular contraction can be adapted to the designed effect is in no instance more remarkable than in the Glottis. The musical pitch of the tones produced by it is regulated by the degree of tension of the *chordæ vocales*, which are possessed of a very considerable degree of elasticity (§ 656). According to the observations of Müller,* the average length of these, in the male, in a state of repose, is about 73-100ths of an inch; whilst in the state of greatest tension it is about 93-100ths; the difference being therefore 20-100ths, or *one-fifth* of an inch: in the female glottis, the average dimensions are about 51-100ths and 63-100ths respectively; the difference being thus about *one-eighth* of an inch. Now the natural compass of the voice in most persons who have cultivated the vocal organ may be stated at about two octaves, or 24 semitones. Within each semitone a singer of ordinary capability could produce at least ten distinct intervals; so that of the total number, 240 is a very moderate estimate. There, must, therefore, be at least 240 different states of tension of the Vocal Cords, every one of which is producible by the will, without any previous trial; and the *whole* variation in the length of the cords being not more than one-fifth of an inch, even in man, the variation required to pass from one interval to another will not be more than 1-1200th of an inch. And yet this estimate is much below that which might be truly made from the performances of a practised vocalist.†

CHAPTER XVI.

OF THE VOICE AND SPEECH.

1. *Of the Larynx, and its Actions.*

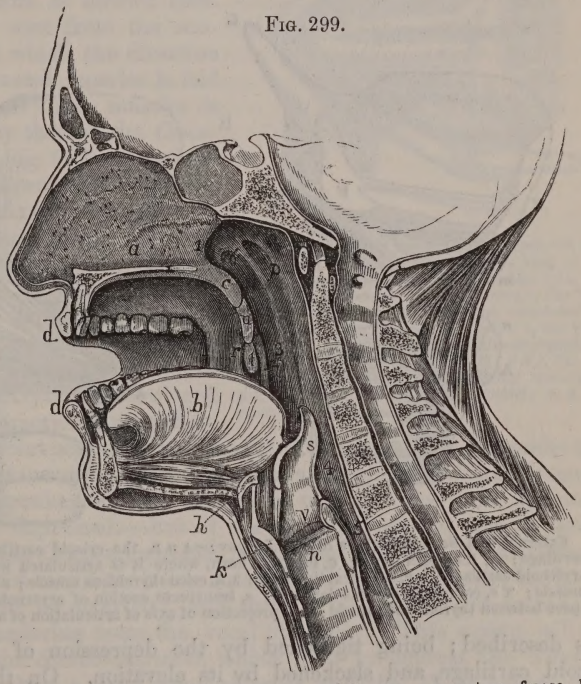
650. THE sounds produced by the Organ of Voice constitute the most important means of communication between Man and his fellows; and the power of Speech has, therefore, a primary influence, as well on his physical condition, as on the development of his mental faculties. It is necessary to

* "Elements of Physiology," Baly's Translation, p. 1018.

† It is said that the celebrated Madame Mara was able to sound 100 different intervals between each tone. The compass of her voice being at least three octaves, or 21 tones, the total number of intervals was 2100, all comprised within an extreme variation of one-eighth of an inch; so that it might be said that she was able to determine the contractions of her vocal muscles to nearly the *seventeen-thousandth* of an inch.

bear in mind that Vocal sounds, and Speech or articulate Language, are two things entirely different; and that the former may be produced in great perfection, where there is no capability for the latter. Hence we might at once infer, that the instrument for the production of vocal sounds is distinct from that by which these sounds are modified into articulate speech; and this we easily discover to be the case, the voice being unquestionably produced in the *larynx*, whilst the modifications of it, by which language is formed, are effected for the most part in the *oral cavity*.—The structure and functions of the former, then, first claim our attention. It will be remembered that the Trachea is surmounted by a stout cartilaginous annulus, termed the *Cricoid* cartilage (Figs. 300, 301, A B, Fig. 302, *r u x w*); which serves as a foundation for the superjacent mechanism. This is embraced (as it were) by the *Thyroid* (Figs. 300, 301, E C G, Fig. 302, G E H), which is articulated to its sides by the lower horns (Figs. 300, 301, c), round the extremities of which it may be considered to turn as on a pivot. In this manner, the lower front border of the Thyroid cartilage which is ordinarily separated by a small interval (Figs. 302, 301, *m n*) from the upper margin of the Cricoid, may be made to approach it or to recede from it; as any one may easily ascertain by placing his finger against the little depression which may be readily felt externally, and observing its changes of size, whilst a range of different tones is sounded; for it will then be noticed that, the higher the note, the more the two cartilages are made to approximate, whilst they separate in proportion to the depth of the tones.* Upon the upper surface of the back of the Cricoid, are seated the two small *Arytenoid* cartilages (Figs. 301, 302, F F); these are fixed in one direction by a bundle of strong ligaments, which tie them to the back of the cricoid; but they have some power of moving in other directions, upon a kind

FIG. 299.



Median Section of *Mouth*, *Nose*, *Pharynx*, and *Larynx*:—*a*, septum of nose; below it, section of hard palate; *b*, tongue; *c*, section of velum pendulum palati; *d*, *d*, lips; *u*, uvula; *r*, anterior arch or pillar of fauces; *i*, posterior arch; *t*, tonsil; *p*, pharynx; *h*, hyoid bone; *k*, thyroid cartilage; *n*, cricoid cartilage; *s*, epiglottis; *v*, glottis; 1, posterior opening of nares; 3, isthmus faucium; 4, superior opening of larynx; 5, passage into œsophagus; 6, mouth of right Eustachian tube.

* In making this observation, it is necessary to put out of view the general movement of the Larynx itself, which the finger must be made to follow up and down.

of articulating suface. The direction of the surface, and the mode in which these cartilages are otherwise attached, cause their movement to be a sort of rotation in a plane which is nearly horizontal, but partly downwards; so that their vertical planes may be made to separate from each other, and at the same time to assume a slanting position. This change of place will be better understood when the action of the muscles is described. To the lower part of the anterior surface of the Arytenoid cartilages are attached the *chordæ vocales* or Vocal Ligaments (Fig. 300, E F, Fig. 302, T V), which stretch across to the front of the Thyroid cartilage; and it is upon the condition and relative situation of these ligaments that their action depends. It is evident that they may be rendered more or less tense by the movement of the Thyroid cartilage

FIG. 300

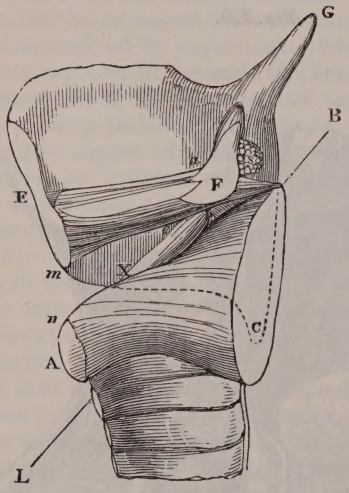
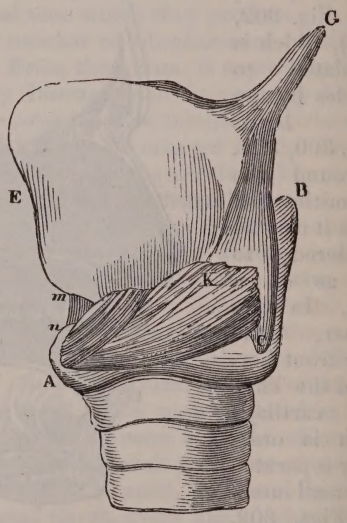


FIG. 301.



External and Sectional views of the *Larynx*:—A *n* B, the cricoid cartilage; E C G, the thyroid cartilage; G, its upper horn; C, its lower horn, where it is articulated with the cricoid; F, the arytenoid cartilage; E F, the vocal ligament; A K, crico-thyroideus muscle; F *e m*, thyro-arytenoideus muscle; X *e*, crico-arytenoideus lateralis; *s*, transverse section of arytenoideus transversus; *m n*, space between thyroid and cricoid; B L, projection of axis of articulation of arytenoid with thyroid.

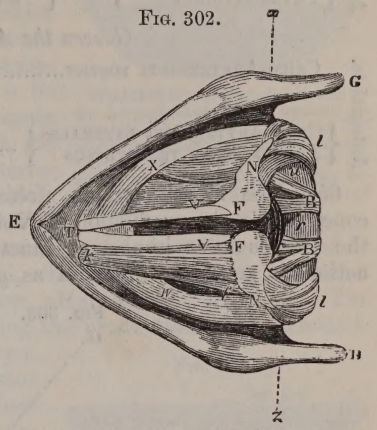
thus described; being tightened by the depression of its front upon the Cricoid cartilage, and slackened by its elevation. On the other hand, they may be brought into more or less close apposition by the movement of the Arytenoid cartilages; being made to approximate nearly, or to recede in such manner as to cause the rima glottidis to assume the form of a narrow V, by the revolution of these cartilages.—We shall now inquire into the actions of the muscles upon the several parts of this apparatus; and first into those of the larynx alone.

651. The depression of the front of the Thyroid cartilage, and the consequent *tension* of the Vocal Ligaments, is occasioned by the conjoint action of the *Crico-thyroidei** (Fig. 301 A K) on both sides; and the chief antagonists to these are the *Thyro-arytenoidei* (Fig. 300, F *m*, Fig. 302, V *k f*), which draw the front of the thyroid back towards the arytenoid cartilages, and thus *relax* the vocal ligaments. These two pairs of muscles may be regarded as the

* For a careful investigation in regard to the precise mode in which the crico-thyroid acts see Jelenffy, Pflüger's "Archiv," 1873, vol. vii. p. 86.

principal governors of the *pitch* of the notes, which, as we shall hereafter see, is almost entirely regulated by the tension of the ligaments; their action is assisted, however, by that of other muscles presently to be mentioned.*—The arytenoid cartilages are made to diverge from each other, by means of the *Crico-arytenoidei postici* (Fig. 302 N *l*) of the two sides, which proceed from their outer corners, and turn somewhat round the edge of the Cricoid, to be attached to the lower part of its back; their action is to draw the outer corners backwards and downwards, so that the points to which the vocal ligaments are attached are separated from one another and the rima glottidis is thrown *open*. This will be at once seen from the succeeding diagram, in which the direction of traction of the several muscles is laid down.—The action of these muscles is partly antagonized by that of the *Crico-arytenoidei laterales* (Fig. 302, N X), which run forwards and downwards from the outer corners of the Arytenoid cartilages, and whose contraction tends to bring their anterior points into the same straight line, depressing them at the same time, so as thus to *close* the glottis. These muscles are assisted by the *Arytenoideus transversus* (Fig. 302), which connects the posterior faces of the Arytenoid cartilages, and which, by its contraction, draws them together. By the conjoint action, therefore, of the Crico-arytenoidei laterales and of the Arytenoideus transversus, the whole of the adjacent faces of the Arytenoid cartilages will be approximated, and the points to which the vocal ligaments are attached will be depressed.—But if the Arytenoideus be put in action in conjunction with the Crico-arytenoidei postici, the tendency of the latter to separate the Arytenoid cartilages being antagonized by the former, its backward action only will be exerted; and thus it may be caused to aid the Crico-thyroidei in rendering tense the vocal ligaments. This action will be further assisted by the *Sterno-thyroidei*, which tend to depress the Thyroid cartilage by pulling from a fixed point below;† and the *Thyro-hyoidei* will be the antagonists of these, when they act from a fixed point above, the Os Hyoides being secured by the opposing contraction of several other muscles.—The respective actions of these muscles will be best comprehended by the following table:—

FIG. 302.



Bird's-eye view of *Larynx* from above:—G E H, the thyroid cartilage, embracing the ring of the cricoid, *r u* X *w*, and turning upon the axis, *x z*, which passes through the lower horns, C, Fig. 300; N F, N F, the arytenoid cartilages, connected by the arytenoideus transversus; T V, T V, the vocal ligaments; N X, the right crico-arytenoideus lateralis (the left being removed); V *k f*, the left thyro-arytenoideus (the right being removed); N *l*, N *l*, the crico-arytenoidei postici; B, B, the crico-arytenoid ligaments.

* Dr. P. Martyn has adduced various observations to show that the Thyroid body exerts an important influence on the pitch of the notes by giving a certain firmness, rigidity, and tension to the larynx. He also suggests that this body may act as a *loader*, rendering the vibrations of the vocal cords slower and longer, and the tone in consequence fuller, louder, and deeper, thus compensating for the small size of the larynx; finally he believes that it aids, by its changes in shape bulk and density, in producing the wonderful qualities of modulation and expression peculiar to the human voice. See "Proceedings of the Royal Society," vol. viii. p. 315.

† These are not usually reckoned among the principal muscles concerned in regulating the voice; but that they are so, any one may convince himself by placing his finger just above the sternum, whilst he is sounding high notes; a strong feeling of muscular tension is then at once perceived.

Govern the Pitch of the Notes.

Antagonists.

Crico-Thyroidei Sterno-Thyroidei	.....	Depress the front of the Thyroid cartilage on the Cricoid, and *stretch* the vocal ligaments; assisted by the Arytenoideus and Crico-arytenoidei postici.
Thyro-Arytenoidei Thyro-Hyoidei	.....	Elevate the front of the Thyroid cartilage, and draw it towards the Arytenoids, *relaxing* the vocal ligaments.

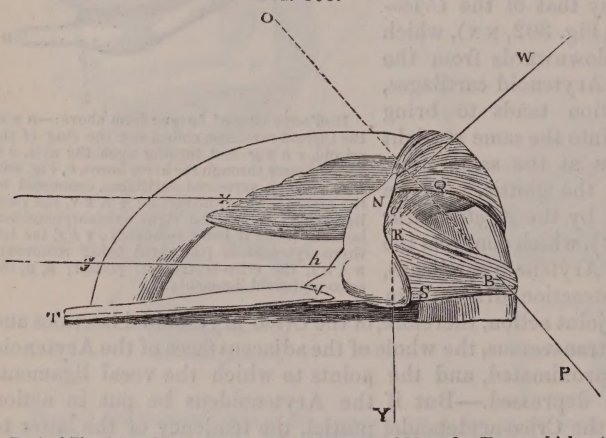
Govern the Aperture of the Glottis.

Antagonists.

Crico-Arytenoidei postici	.....	*Open* the Glottis.
Crico-Arytenoidei laterales Arytenoideus transversus	.....	Press together the inner edges of the Arytenoid cartilages, and *close* the Glottis.

652. The muscles which stretch or relax the Vocal cords are entirely concerned in the production of Voice: those which govern the aperture of the Glottis have important functions in connection with the Respiratory actions in general, and stand as guards (so to speak) at the entrance to the lungs. These separate actions are easily made evident. In the ordinary condition of rest, it seems probable that the Arytenoid cartilages are considerably separated from each other; so as to cause a wide opening to intervene between their inner faces and between the vocal ligaments, through which the air freely passes; and the vocal ligaments are at the same in a state of complete relaxation.—We can close the aperture of the Glottis by an exertion of the will, during either inspiration or expiration; and its closure by an automatic impulse forms part of the acts of Coughing and Sneezing (§ 280), besides giving rise to those more prolonged impediments to the ingress and egress of air, which have been already noticed as resulting from disordered states of the Nervous system. With these actions, the muscles which regulate the tension of the vocal ligaments have nothing to do; and we have seen that they are performed by the instrumentality of the Pneumogastric or proper Respiratory nerve (§ 276). The appearances which present themselves when the interior of the Larynx is examined during life are, according to Professor Czermak, that in the almost semi-lunar space bounded by the posterior wall of the Pharnyx (Fig. 304) and the base of the tongue, the upper curved edge of the epiglottis (*e*) is seen, its lateral portions just touching the posterior pharnygeal wall, and its central portion arching forwards, so as to leave an interval for the passage of air in the median line.

Fig. 303.



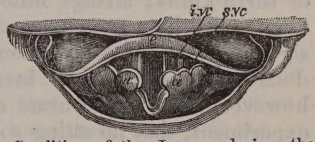
Part of Fig. 302 enlarged, to show the *Direction of Muscular Forces* which act on the Arytenoid cartilage: N V S, the right Arytenoid cartilage; T, V, its vocal ligament; B R S, bundle of ligaments uniting it to Cricoid; O P, projection of its axis of articulation; *h g*, direction of the action of the Thyro-arytenoideus; N X, direction of Crico-arytenoideus lateralis; N W, direction of Crico-arytenoideus posticus; N Y, direction of Arytenoideus transversus.

Near the centre of the cleft between the upper border of the epiglottis and the walls of the pharynx, a tranverse band or cushion (*c*) is also seen, of a reddish colour, and formed by the edge of the fold of mucous membrane sustained between the two separated arytenoid cartilages (*aa*). The anterior outline of the fold is concave in front, and forms with the superior border of the epiglottis, which is concave behind and situated a little higher, a narrow transversely-elliptical fissure. If the vowel *a* be now sounded as in *ah* or *eh*, the semilunar space behind the base of the tongue is enlarged, the epiglottis rises and separates from the posterior wall of the pharynx, the glottis becomes widely opened, and a considerable portion of the anterior wall of the trachea can be perceived. A small rounded swelling situated to the outer side of the tubercles of Santorini, which was previously concealed by the lateral border of the epiglottis, now also comes into view. The movements of the arytenoid cartilages during the production of vocal sounds can be very distinctly observed by the laryngoscope, and the account given by Professor Czermak possesses considerable interest, since it fully corroborates the views derived from theory and experiment on the dead subject, which had been expressed before the introduction of the instrument. As soon as we wish to utter a sound, the two arytenoid cartilages raise themselves in the fold of mucous membrane which covers them, and approach one another with surprising mobility. This movement effects the approximation of the vocal cords, and consequently the constriction of the Glottis (Fig. 305.) The study of the mode of formation of the gravest chest-sounds is extremely difficult, on account of the arytenoid cartilages becoming elevated and rapidly approaching one another until they come almost into complete contact, whilst they bend under the border of the depressed epiglottis in such a manner that the latter, as viewed by the laryngoscope, entirely conceals the interior of the Larynx. According to Mandl* the opening of the glottis in the production of the deepest notes is ellipsoidal. During the emission of the most acute sounds, the Glottis is contracted in a linear form (Fig. 306); on each side we perceive the vocal cords, distinguished by their whitish-yellow colour, and a little to the outer side is a narrow groove indicating the position of the ventricles of Morgagni. Further outwards again are the false or superior vocal cords. These parts, with the erected arytenoid cartilages, the epiglottis pulled upwards and forwards, and the aryteno-epiglottidian ligaments, together form a short and stiff tube situated above the Glottis; the whole appearing, from the sensation we experience during the experiment,

FIG. 304.

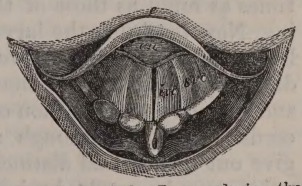
Condition of the *Larynx* as seen by the Laryngoscope during tranquil respiration: *e*, epiglottis; *œ*, fissure-like opening of œsophagus; *c*, fold of mucous membrane bounding the opening of the glottis posteriorly, and extending between the tubercles of the cartilages of Santorini.

FIG. 305.



Condition of the *Larynx* during the emission of the broad vowel sound (A): *a*, cartilages of Santorini surmounting the arytenoid cartilages; *e*, epiglottis; *i v c*, inferior or true vocal cord; *s v c*, superior or false vocal cord of right side.

FIG. 306.



Condition of the *Larynx* during the emission of a high or acute sound: *e*, epiglottis; *cu*, cushion of epiglottis; *i v c*, true vocal cord; *s v c*, false vocal cord.

* "Wien Acad. Sitz.-ber.," Band lxii. p. 764; and "Traité Pratique des Maladies du Larynx et du Pharynx," Paris, 1872.

to be in a state of very great tension.* That the aperture of the glottis is greatly narrowed during the production of sounds, is easily made evident to one's-self, by comparing the time occupied by an ordinary expiration, with that required for the passage of the same quantity of air during the sustenance of a vocal tone. Further, the size of the aperture is made to vary in accordance with the note which is being produced; of this, too, any one may convince himself, by comparing the times during which he can hold out a low and a high note; from which it will appear that the aperture of the glottis is so much narrowed in producing a high note, as to permit a far less rapid passage of air than is allowed when a low one is sounded. According to Kempelen no sound is elicited when the distance between the Chordæ Vocales exceeds 1-10th to 1-12th of an inch. The muscular movements concerned in the act of vocalization appear to be called-forth by the instrumentality of the motor fibres, partly derived from the Spinal Accessory nerve, which are contained in Pneumogastric (§ 452).

653. We have now to inquire what is the operation of the Vocal Cords in the production of sounds; and in order to comprehend this, it is necessary to advert to the conditions under which tones are produced by instruments of various descriptions having some analogy with the Larynx. These are chiefly of three kinds; strings, flute-pipes, and reeds or tongues.—The Vocal Ligaments were long ago compared by Ferrein to vibrating *strings;* and at first sight there might seem a considerable analogy, the sounds which both produce being elevated by increased tension. This resemblance disappears, however, on more accurate comparison; for it may be easily ascertained by experiment, that no string so short as the vocal ligaments could give a clear tone at all to be compared in depth with that of the lowest notes of the human voice; and also, that the scale of changes produced by increased tension is fundamentally different. When strings of the same length but of different tensions are made the subject of comparison, it is found that the number of vibrations is in proportion to the square-roots of the extending forces. Thus, if a string extended by a given weight produce a certain note, a string extended by four times that weight will give a note in which the vibrations are twice as rapid; and this will be the octave of the other. If nine times the original weight be employed, the vibrations will be three times as rapid as those of the fundamental note, producing the twelfth above it. Now by fixing the larynx in such a manner that the vocal ligaments can be extended by a known weight, Müller has ascertained that the sounds produced by a variation of the extending force do not follow the same ratio; and therefore the condition of these ligaments cannot be simply that of vibrating cords. Further, although a cord of a certain length, which is adapted to give out a clear and distinct note equal in depth to the lowest of the human voice, may be made by increased tension to produce all the superior notes (which, in stringed instruments, are ordinarily obtained by shortening the strings), it does not follow that a short string, which, with moderate tension, naturally produces a high note, should be able, by a diminution of the tension, to give out a deep one; for, although this might be theoretically possible, yet it cannot be accomplished in practice; since the vibrations become irregular on account of the diminished elasticity.† These considerations

* "On the Laryngoscope," Syd. Soc. Trans., 1861, pp. 37–8; see also "The Laryngoscope," by George D. Gibb, M.D., London, 1863. Morell Mackenzie, M.D., "The Use of the Laryngoscope, 3rd edit., 1869.

† Thus it would be impossible to produce good Bass notes on the strings of a Violin by diminishing their tension; the length afforded by the Violoncello or Double Bass is requisite.

are in themselves sufficient to destroy the supposed analogy; and to prove that the Chordæ Vocales cannot be reduced to the same category with vibrating strings.

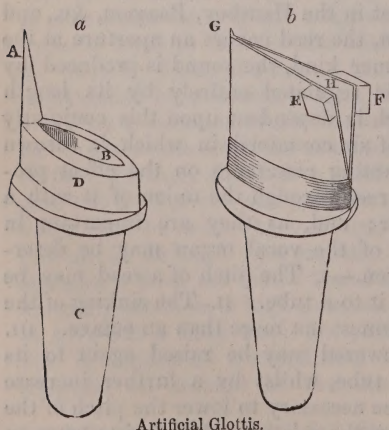
654. The next kind of instrument with which some analogy might be suspected, is the *flute-pipe*, in which the sound is produced by the vibration of an elastic column of air contained in the tube; and the pitch of the note is determined almost entirely by the length of the column, although slightly modified by its diameter, and by the nature of the embouchure or mouth from which it issues. This is exemplified in the German Flute, and in the English Flute or Flageolet; in both of which instruments the acting length of the pipe is determined by the interval between the embouchure and the nearest of the side-apertures; by opening or closing which, therefore, a modification of the tone is produced. In the Organ, of which the greater number of pipes are constructed upon this plan, there is a distinct pipe for every note; and their length increases in a regular scale. It is, in fact, with flute-pipes as with strings—that a diminution in length causes an increase in the number of vibrations, in a simply-inverse proportion; so that of two pipes, one being half the length of the other, the shorter will give a tone which is the octave above the other, the vibrations of its column of air being twice as rapid. Now there is nothing in the form or dimensions of the column of air between the larynx and the mouth, which can be conceived to render it at all capable of such vibrations as are required to produce the tones of the Human voice; though there is some doubt whether it be not the agent in the musical tones of certain Birds. The length that would be required in an open pipe to give the lowest G of the ordinary bass voice, is nearly six feet; and the conditions necessary to produce the higher notes from it, are by no means those which we find to exist in the process of modulating the human voice.

655. We now come to the third class of instruments, in which sound is produced by the vibration of *reeds* or *tongues;* these may either possess elasticity in themselves, or be made elastic by tension. The 'free' reeds of the Accordion, Concertina, Seraphine, Harmonium, &c., are examples of instruments of this character, in which the lamina vibrates in a sort of frame that allows the air to pass out on all sides of it through a narrow channel, thus increasing the strength of the blast: whilst in the Hautboy, Bassoon, &c., and in the Organ-pipes of similar construction, the reed covers an aperture at the side of one end of a pipe. In the former kind, the sound is produced by the vibration of the tongue alone, and is regulated entirely by its length and elasticity; whilst in the latter its pitch is dependent upon this conjointly with the length of the tube, the column of air contained in which is thrown into simultaneous vibration. Some interesting researches on the effect produced on the pitch of a sound given by a reed through the union of it with a tube, have been made by M. W. Weber; and, as they are important in furnishing data by which the real nature of the vocal organ may be determined, their chief results will be here given.—I. The pitch of a reed may be lowered, but cannot be raised, by joining it to a tube. II. The sinking of the pitch of the reed thus produced is at the utmost not more than an octave. III. The fundamental note of the reed thus lowered may be raised again to its pitch by a further lengthening of the tube, whilst by a further increase it is again lowered. IV. The length of tube necessary to lower the pitch of the instrument to any given point, depends on the relation which exists between the frequency of the vibrations of the tongue of the reed, and those of the column of air in the tube, each taken separately.—From these data, and from those of the preceding paragraph, it follows that if a wind instrument can, by

the prolongation of its tube, be made to yield tones of any depth in proportion to the length of the tube, it must be regarded as a flute-pipe ; whilst if its pitch can only be lowered an octave or less (the embouchure remaining the same) by lengthening the tube, we may be certain that it is a reed instrument. The latter proves to be the case in regard to the Larynx.

656. It is evident from the foregoing considerations, that the action of the Larynx has more analogy to that of *reed* instruments, than it has to that either of vibrating *strings*, or of *flute-pipes ;* and though there would seem, at first sight, to be a marked difference in character between the vocal ligaments and the tongue of any reed instrument, this difference is really by no means considerable. In a reed, elasticity is a property of the tongue itself, when fixed at one end, the other vibrating freely ; but by a membranous lamina, fixed in the same manner, no tone would be produced. If such a lamina, however, be made elastic by a moderate degree of tension, and be fixed in such a manner as to be advantageously acted on by a current of air, it will give a distinct tone. It is observed by Müller, that membranous tongues made elastic by tension may have either of three different forms :—I. That of a band extended by a cord, and included between two firm plates, so that there is a cleft for the passage of air on each side of the tongue. II. The elastic membrane may be stretched over the half or any portion of the end of a short tube, the other part being occupied by a solid plate, between which and the elastic membrane a narrow fissure is left. III. Two elastic membranes may be extended across the mouth of a short tube, each covering a portion of the opening, and having a chink left open between them.—This last is evidently the form most allied to the Human Glottis ; but it may be made to approximate still more closely, by prolonging the membranes in a direction parallel to that of the current of air, so that not merely their edges, but their whole planes shall be thrown into vibration. Upon this principle, a kind of *artificial glottis* has been constructed by Mr. Willis ; the conditions of action and the effects of which are so nearly allied to that of the real instrument, that the similar character of the two can scarcely be doubted. The following is his description of it :—"Let a wooden pipe be prepared of the Form of Fig. 307, *a*, having a foot, C, like that of an organ-pipe, and an upper opening, long and narrow, as at B, with a point, A, rising at one end of it. If a piece of leather, or still better, of sheet India-rubber, be doubled round this point, and secured by being bound round the pipe at D with strong thread, as in Fig. 307, *b*, it will give us an artificial glottis with its upper edges G H, which may be made to vibrate or not, at pleasure, by inclining the planes of the edges. A couple of pieces of cork, E F, may be glued to the corners, to make them more manageable. From this machine various notes may be obtained, by stretching the edges in the direction of their length G H ; the notes rising in pitch with the increased tension, although the length of the vibrating edge is increased. It is true that a scale of notes equal in extent to that of the human voice cannot be obtained from edges of leather ; but this scale is much greater in India-rubber than in leather, and the elasticity of them both

Fig. 307.



Artificial Glottis.

is so much inferior to that of the vocal ligaments, that we may readily infer that the greater scale of the latter is due to its greater elastic powers." By other experimenters the tissue forming the middle coat of the arteries has been used for this purpose, in the moist state, with great success; with this, the tissue of the vocal ligament is nearly identical. It is worthy of remark, that, in all such experiments, it is found that the two membranes may be thrown into vibration, when inclined *towards* each other in various degrees, or even when they are in parallel planes, and their edges only approximate; but that the least inclination *from* each other (which is the position the vocal ligaments have during the ordinary state of the glottis (§ 651–652), completely prevents any sonorous vibrations from being produced.

657. The pitch of the notes produced by membranous tongues may be affected in several ways. Thus, an increase in the strength of the blast, which has little influence on metallic reeds, raises *their* pitch very considerably; and in this manner the note of a membranous reed may be raised by semitones, to as much as a fifth above the fundamental. The addition of a pipe has nearly the same effect on their pitch, as on that of metallic reeds; but it cannot easily be determined with the same precision. Several different notes may be produced with a pipe of the same length; but there is a certain length of the column of air, which is the one best adapted for each tone. It has been recently ascertained, moreover, that the length of the pipe prefixed to the reed has a considerable influence on its tone, rendering it deeper in proportion as it is prolonged, down to nearly the octave of the fundamental note; but the pitch then suddenly rises again, as in the case of the tube placed beyond the reed. The researches of Müller, however, have not succeeded in establishing any very definite relation between the lengths of the two tubes in regard to their influence on the pitch of the reed placed between them. Oertel* has shown by the stroboscopic method of observation† that in ordinary chest tones the vocal cords vibrate throughout their whole length and breadth, in such a way that the excursions of the various points of the cord increase with their distance from the outer border.

658. From the foregoing statements, it appears that the true theory of the Voice may now be considered as well established, in regard to this essential particular—that the sound is the result of the vibrations of the true vocal cords, which take place according to the same laws with those of metallic or other elastic tongues: and that the pitch of the notes is chiefly governed by the tension of these laminæ. With respect, however, to the mode and degree in which these tones are modified by the shape of the air-passages both above and below the larynx, by the force of the blast and by other concurrent circumstances, little is certainly known; but no doubt can be felt that these

* "Centralblatt," 1878, pp. 81 and 89.

† This consists in observing a body having a rapid but unknown rate of vibration at intervals which can be regulated to correspond to the unknown rate. This object can be accomplished by illuminating the vibrating body by a rapid series of electrical sparks, or by looking at it through holes in the edge of a revolving disk, or through a perforated disk attached to a tuning-fork. If the rate of the observations coincides with that of the vibrating body, the latter, being observed always in the same phase of its vibration, presents the appearance owing to the persistence of the impressions on the retina of a body perfectly at rest. If the rate of the observations be a little slower than that of the vibrating body, the latter, being at each observation in a somewhat more advanced phase of its movement, will appear to execute its vibration at a rate corresponding to the difference between the rates of observation and vibration. Thus a body vibrating two hundred times in a second, seen through a stroboscopic apparatus, giving two hundred and one observations in a second, will appear to vibrate once in a second. Thus by knowing the rate of the observations, and noting the rate of the apparent stroboscopic movement, the rate of the vibrating body may be determined.

modifications are of great importance, when we observe the great amount of muscular action which takes place consentaneously with the production of vocal tones, and which seems designed to alter the length and tension of the various parts of the *vocal tube*, so that they may vibrate synchronously with the *vocal cords*. Thus, during the ascent of the voice from the deeper to the higher notes of the scale, we find the whole larynx undergoing an elevation towards the base of the cranium, the thyroid cartilage being drawn up within the oshyoides, so as even to press on the epiglottis ; at the same time, the small space between the thyroid and cricoid cartilages, or crico-thyroid chink, is closed by the depression of the front of the former upon the latter (§ 651); the velum palati is depressed and curved forwards; and the tonsils approach one another. The reverse of all these movements takes place during the descent of the voice.—A very important adjunct to the production of the higher notes has been pointed out by Müller, as being afforded by the modification in the space included between the two sides of the thyroid cartilage, which is effected by the thyro-arytenoidei. He had experimentally ascertained that the introduction of a hollow plug into the upper end of the pipe beneath his artificial larynx (and therefore just below the reed), by diminishing its aperture, produced a considerable elevation of the tone. The action may be imitated in the human larynx, when made the subject of experiment, by compressing the thyroid cartilage laterally; and in this manner, the natural voice can be made to extend through a range that could otherwise be only reached by a falsetto. The influence of the prefixed and superadded tubes, in modifying the tones produced by the Human larynx, has been found by Prof. Müller not to be at all comparable to that which they exercised over the artificial larynx; the reason of which difference does not seem very apparent. It appears, however, that there is a certain length of the prefixed tube—as there is a certain distance of the vibrating laminæ, and a certain length or form of the tube above—which is most favourable to the production of each note; and the downward movement of the whole vocal organ, which takes place when we are sounding deep notes, and its rise during the elevation of the tones, have been supposed to answer the purpose of making this adjustment in the length of the trachea; but this requires the supposition that the real length of the trachea is shortened whilst it appears extended—for which there seems no foundation. It is considered by Mr. Wheatstone, that the column of air in the trachea may divide itself into 'harmonic lengths,' and may produce a *reciprocation* of the tone given by the vocal ligaments; and in this manner he considers that the falsetto notes are to be explained. It may be added that the partial closing of the epiglottis seems to assist in the production of deep notes, just as the partial covering of the top of a short pipe fixed to a reed will lower its tone; and that something of this kind takes place during natural vocalization, would appear from the retraction and depression of the tongue, which accompany the lowering of the front of the head when the very lowest notes are being sounded. The experiments of Savart have shown that a cavity which only responds to a shrill note, when its walls are firm and dry, may be made to afford a great variety of lower tones, when its walls are moistened and relaxed in various degrees. This observation may probably be applied also to the trachea.

659. The *falsetto* is a peculiar modification of the voice, differing from the 'chest-voice,' not merely in the higher pitch of its notes, but also in their quality; its tones being less ready, and more like the 'harmonic notes' of stringed and wind instruments. In some individuals, the chest-voice passes by imperceptible gradations into the falsetto, whilst in others the transition is

abrupt; and some persons can sound the same notes in the two different registers, these notes forming the upper part of the scale of the chest-voice, and the lower part of the falsetto.*—With regard to the theory of the production of the falsetto voice, there has been considerable difference of opinion amongst Physiologists; and it cannot be regarded as fully determined. By Magendie and Mayo it was maintained that these tones are produced by the vibration of the vocal cords along only part of their length, the rima glottidis being partly closed; and this explanation is consistent with the fact, that a far smaller quantity of air is required for sustaining a falsetto note, than for a note of the ordinary register, even though they should be of the same pitch. By Müller and Garcia,† again, it is asserted that in the production of the falsetto notes, merely the thin border of the glottis vibrates, since the fibres of the lateral crico-arytenoid muscle remain inactive, whilst the lips of the glottis, stretched by the horizontal bundle of the thyro-arytenoid, come in contact by their edge alone, and offer little resistance to the air. In the chest-voice, on the contrary, the contraction of the lateral crico-arytenoids gives a rotatory movement to the cartilages, and increases the depth of the surface of contact of the two ligaments, and it is to this circumstance that the peculiar amplitude of the notes of the chest-register is attributable. Mandl believes that both these doctrines are correct: and that in the production of falsetto notes, the false or upper vocal cords apply themselves to the true vocal cords in front, behind, and to the sides, so that the middle portion of the true cords alone vibrates; whilst by the contraction of the arytenoid muscles the cords are brought into close apposition‡ with each other for part of their length, their thin edges only being in vibration in the remainder. Oertel,§ again, employing the stroboscopic method of observation, finds that in falsetto tones, on the other hand, though the cords vibrate in their whole length and breadth, the vibrating surface presents a curved nodal line about one-third of the distance from the free edge to the attached border, the parts of the cord on opposite sides of the nodal line being of course in opposite phases of vibration. In very high falsetto tones a second nodal line may be observed, indicating a still further subdivision of the vibrating surface. It has been pointed out by Mr. Bishop (loc. cit.), that at the moment of transition from the 'chest-voice' to the 'falsetto-voice,' the crico-thyroid chink, which was closed during the production of the highest note of the former, suddenly opens on the production of the lowest note of the latter, thus indicating that the vocal cords are *relaxed* in the passage from the one to the other, as must be the case, if, for the production of the same note, they be only put in vibration along a part of their length; so that it would not seem improbable that the cause of those differences in the mode of transition, which have been already noticed, lies in the differences in the proportional amount of the vocal cords, which is thus thrown out of use by the partial approximation of the two lips of the rima glottidis. It is further remarked by Mr. Bishop, that, in the passage from the chest- to the falsetto-voice, the larynx descends from its previously

* Thus, a gentleman of the Author's acquaintance has a bass voice of a harsh reedy character, ranging from the D below the bass clef to the D above it (two octaves); whilst his falsetto, which is remarkable for its clearness and smoothness, ranges from the A on the highest line of the bass clef to the E in the highest space of the treble clef. Hence there are five notes common to the two registers, and the entire voice ranges through more than three octaves; but, from want of a gradual passage from one to the other, this gentleman can only sing bass parts with his chest voice, or alto parts with his falsetto, the tenor scale extending above the range of one, and below that of the other.

† "Proceedings of the Royal Society," vol. vii. p. 408.

‡ See also Ch. Bataille, "Nouv. Réch. sur la Phonation," Paris, 1861. § Op. cit.

elevated position, and gradually rises again with the ascending scale of falsetto notes; and he mentions a case of *double falsetto*, in which a third register existed, and in which the relaxation of the vocal cords and the descent of the larynx were observed at its commencement, as at the commencement of the secondary or ordinary falsetto register.* Michael's† experiments, which were chiefly made on patients affected with paralysis, seem to show that, in singing, all the glottidean muscles are brought into play, though, with different registers, different muscles are specially exerted. None of the three registers require the full action of all the muscles, but with each register one particular muscle is in full action, thus giving the register its klang tone. In the chest register the crico-arytenoideus lateralis is chiefly in action, and the whole vocal cord vibrates; in the middle and falsetto registers only a part of the vocal cord vibrates. The tone-giving muscle of the middle register is the thyro-arytenoideus internus, whilst in the falsetto, the cricothyroid is alone in full contraction. The klang tone of the falsetto results from the thyro-arytenoid being relaxed, and the closure of the resulting elliptical slit is effected by the cricothyroid. The cricothyroid is supplied by a special nerve, and hence often remains functionally active when the other glottidean muscles are paretic. The pressure of the air within the trachea during the production of voice is considerable. Cagniard de Latour observed in a man with a tracheal fistula, that the pressure indicated by a manometer when the patient called out at the top of his voice, was equal to a column of water 38 inches in height; when he spoke at his usual pitch, to one of 5 inches; and when he sang a high note, to one of about 8 inches. The deepest notes the human Larynx is capable of producing have about 80 double vibrations in the second, the highest about 992; the former occurring in bass, the latter in soprano voices. Donders‡ gives the limits at 44 vibrations, corresponding to the F of the lowest bass voice, and 1408 for the highest note corresponding to the highest f''' of the soprano, which includes 5 octaves.

660. The various muscular actions which are employed in the production and regulation of the Voice are called forth by an impulse which has been shown (§ 496) to be really *automatic* in its operation, and to be completely under the influence of guiding sensations, although usually originating in a Volitional determination, or giving expression to Emotions or simply to Ideas. This, however, has been proved to be also true of *all* Volitional movements; so that the production of vocal tones constitutes no real exception. It may be safely affirmed that the simple utterance of sounds is in itself an Instinctive act; although the combination of these, whether into music or into articulate language, is a matter of acquirement, which is much more readily made by some individuals than by others. No definite tone can be produced by a Voluntary effort, unless that tone be present to the consciousness during an interval—however momentary—either as immediately produced by an act of Sensation, recalled by an act of Conception, or anticipated by an effort of the Imagination. When thus present, the Will can enable the muscles to

* An entirely different theory of the falsetto has been given, however, by MM. Pétrequin and Diday ("Gazette Médicale," 1844), who consider that the falsetto notes are not produced by the vibration of the vocal cords, but are really 'flute-notes,' formed by the vibrations of the column of air to which the rima glottidis then serves as the embouchure. This view harmonizes well with some of the phenomena of the falsetto voice; but it is open to the objections already stated in regard to the flute theory generally. It may be added that some have attempted to show that the falsetto depends upon a peculiar action on the parts *above* the larynx; but for this doctrine there is no foundation whatever.

† "Berlin, Klinisch. Wochensch," 1876, Nos. 36 and 37; "Centralblatt," 1877, p. 26.

‡ Dr. Moore's Translation in Humphry and Turner's "Journ. of Anat. and Physiology," vol. i. 1867, p. 173.

assume the condition requisite to produce it; but under no other circumstances does this happen, except through the particular mode of discipline by which the congenitally deaf may be trained to speak. Such persons are debarred from learning the use of Voice in the ordinary manner; for the necessary guidance cannot be afforded, either through sensations of the present or conceptions of the past, and the imagination is entirely destitute of power to suggest that which has been in no shape experienced. But they may be taught to acquire an imperfect speech, by causing them to imitate particular muscular movements, which they may be made to see; being guided in the imitation of those movements, in the first place by watching their own performance of them in a looking-glass, and afterwards by attending to the muscular sensations which accompany them. Many instances, indeed, are on record, in which persons entirely deaf were enabled to carry on a conversation in the regular way; judging of what was said by the movements of the lips and tongue, which they had learned to connect with particular syllables; and regulating their own voices in reply, by their voluntary power, guided in its exercise by their muscular sensations.*

2. *Of Articulate Sounds.*

661. The Larynx, as now described, is capable of producing those *tones* of which Voice fundamentally consists, and the sequence of which becomes Music: but *Speech* consists in the modification of the laryngeal tones, by other organs intervening between the Glottis and the Os externum, so as to produce those *articulate sounds* of which language is formed. It cannot be questioned that Music has its language; and that it is susceptible of expressing Emotional states of the mind (among those, at least, who have been accustomed to associate these with its varied modes) to even a higher degree than articulate speech. But it is incapable of addressing the Intellect, by conveying definite ideas of objects, properties, actions, &c., in any other way than by a kind of imitation, which may be compared to the signs used in hieroglyphic writing. These ideas it is the peculiar province of Articulate Language to convey; and we find that the vocal organ is adapted to form a large number of simple sounds, which may be readily combined into groups, forming words. The number of combinations which can be thus produced is so inexhaustible, that every language has its own peculiar series; no difficulty being found in forming new ones to express new ideas. There is considerable diversity in different languages, even with regard to the use of the simplest of these combinations; some of them are more easy of formation than others, and these accordingly enter into the composition of all languages; whilst of the more difficult ones, some are employed in one language, some in another —no one language possessing them all. Without entering into any detailed account of the mechanism required to produce each of these simple sounds, a few general considerations will be offered in regard to the classification of them; and the peculiar defect of articulation termed *Stammering* will be briefly treated of.

662. Vocal sounds are divided into Vowels and Consonants; and the distinctive characters of these are usually considered to be, that the Vowels are produced by the Voice alone, whilst the sound of the Consonant is formed by some kind of interruption to the voice, so that they cannot be properly expressed unless conjoined with a vowel. The distinction may be more correctly laid down, however, in this manner:—the Vowel sounds are continuous

* See Dr. Johnstone "On Sensation," p. 128.

tones, modified by the form of the aperture through which they pass out; whilst in sounding Consonants the breath suffers a more or less complete interruption in its passage through parts anterior to the larynx. Hence the really simple Vowel sounds are capable of prolongation during any time that the breath can sustain them; this is not the case, however, with the real Diphthongal sounds (of which it will presently appear that the English *i* is one); whilst it is true of some Consonants. It seems to have been forgotten by many of those who have written upon this subject, that the laryngeal voice is not essential to the formation of either vowels or consonants; for all may be sounded in a whisper. It is very evident, therefore, that the larynx is not primarily concerned in their production; and this has been fully established by the following experiment. A flexible tube was introduced by M. Delau through the nostril into the pharynx, and air was impelled through it into the fauces; then, closing the larynx, he threw the fauces into the different positions requisite for producing articulate sounds, when the air impelled through the tube became an audible whisper. The experiment was repeated, with this variation, that the laryngeal sounds were allowed to pass into the fauces; and each articulated letter was then heard double, in a proper voice, and in a whisper. Observations* made by Professor Moore upon those who from some cause are unable to transmit the air which has passed through the trachea and aperture of the glottis into the mouth, have demonstrated (1) that the larynx is the seat of vocalization for the vowels *a* in all its forms, *i* long, *o* long, and the pure aspirate; also for the short vowels which are to some extent explosive, as *i* in sit, *o* in not, and *e* in err, though the last can also be made in the front part of the mouth. With the exception of the pure breathing and the short vowels, all these sounds receive a finish in the pharynx, nose, and mouth. (2) That the vowels *e* long and *oo*, the diphthong *eu*, which is made up of these two elements, and all the consonants, are made above the larynx.

663. That the Vowels are produced by simple modifications in the form of the external passages, is easily proved both by observation and by imitative experiment. When the mouth is opened wide, the tongue depressed, and the velum palati elevated, so as to give the freest possible exit to the voice, the vowel *a* in its broadest form (as in *ah*) is sounded.† On the other hand, if the oral aperture be contracted, the tongue being still depressed, the sound *oo* (the Continental *u*) is produced. If attention be paid to the state of the buccal cavity, during the pronunciation of the different vowel-sounds, it will be found to undergo a great variety of modifications, arising from varieties of position of the tongue, the cheeks, the lips, and velum palati. The position of the tongue is, indeed, one of the primary conditions of the variation of the sound; for it may be easily ascertained that, by peculiar inflections of this organ, a great diversity of vowel-sounds may be produced, the other parts remaining the same. Still there is a certain position of all the parts which is most favourable to the formation of each of these sounds; but this could not be expressed without a lengthened description. The following table, slightly altered from that of Kempelen, expresses the relative dimensions of the buccal *cavity* and of the *orifice* for some of the principal of these; the number 5 expressing the largest size, and the others in like proportion :—

* See the interesting paper of Prof. E. M. Moore, "New York Medical Record," vol. vii. 1872, p. 49.

† This sound of the vowel *a* is scarcely used in our language, though very common in most of the Continental tongues; the nearest approach to it in English is the *a* in far; but this is a very perceptible modification, tending towards *au*.

Vowel.	*Sound.*	*Size of oral opening.*	*Size of buccal cavity.*
a . . .	as in *ah*	5	5
a . . .	as in *name*	4	2
e . . .	as in *theme*	3	1
o . . .	as in *cold*	2	4
oo . . .	as in *cool*	1	5

These are the sounds of the five vowels, *a*, *e*, *i*, *o*, *u*, in most Continental languages; and it cannot but be admitted that the arrangement is a much more natural one than that of our own vowel series. The English *a* has three distinct sounds capable of prolongation;*—the true broad *a* of *ah*, slightly modified in *far;* the *a* of *fate*, corresponding to the *e* of French; and the *a* of *fall*, which should be really represented by *au*. This last is a simple sound, though commonly reckoned as a diphthong. In Kempelen's scale, the oral orifice required to produce it would be about 3, and the scale of the buccal cavity 4.† On the other hand, the sound of the English *i* cannot, like that of a true vowel, be prolonged *ad libitum;* it is in fact a sort of diphthong, resulting from the transition from a peculiar indefinite murmur to the sound of *e*, which takes its place when we attempt to continue it. The sound *oy* or *oi*, as in *oil*, is a good example of the true diphthong; being produced by the transition from *au* to *e*. In the same manner the diphthong *ou*, which is the same with *ow* in owl, is produced in the rapid transition from the broad *a* of *ah*, to the *oo* of cool.—Much discussion has taken place as to the true character of *y*, when it commences a word, as in yet, yawl, &c., some having maintained that it is a consonant (for the very unsatisfactory reason that we are in the habit of employing *a* rather than *an*, when we desire to prefix the indefinite article to such words), whilst others regard it as a peculiar vowel. A slight attention to the position of the vocal organs during its pronunciation, makes it very clear that its sound in such words really corresponds with that of the long (English) *e;* the pronunciation of the word yawl being the same as that of ēaul, when the first sound is not prolonged, but rapidly transformed into the second. The sound of the letter *w*, moreover, is really of the vowel character, being formed in the rapid transition from *oo* to the succeeding vowel; thus *wall* might be spelt *o͞oal*. Many similar difficulties might be removed, and the conformity between spoken and written language might be greatly increased (so as to render far more easy the acquirement of the former from the latter), by due attention to the state of the vocal organs in the production of the simple sounds.

664. It is not very difficult to produce a tolerably good artificial imitation of the Vowel-sounds. The method adopted by Helmholtz of combining the fundamental note with various harmonics for each vowel has been already referred to (§ 599). By Kempelen it was accomplished by means of an India-rubber ball, with an orifice at each end, of which the lower one was attached to a reed: by modifying the form of the ball, the different vowels could be sounded during the action of the reed. He also employed a short funnel-like tube, and obtained the different sounds by covering its wide opening to a greater or less extent. This last experiment has been repeated by

* The *short* vowel sounds, as *a* in fat, *e* in met, *o* in pot, &c., are not capable of prolongation.

† The mode of making a determination of this kind may here be given for the sake of example. If the broad *a* be sounded, the mouth and fauces being opened wide, and we contract the oral orifice by degrees, at the same time slightly elevating the point of the tongue, we gradually come to the sound of *au;* by still further contracting the orifice, and again depressing the tongue, we form *oo*. On the other hand, in sounding *e*, the tongue is raised nearly to the roof of the mouth; if it be depressed, without the position of the lips being altered, *au* is given.

Mr. Willis; who has also found that the vowel-sounds might be imitated by drawing-out a long straight tube from the reed. In this experiment he arrived at a curious result:—with a tube of a certain length, the series of vowels, *i*, *e*, *a*, *o*, *u*, was obtained by gradually drawing it out; but if the length was increased to a certain point, a further gradual increase would produce the same sequence in an inverted order, *u*, *o*, *a*, *e*, *i*; a still further increase would produce a return to the first scale, and so on. When the pitch of the reed was high, and the pipe short, it was found that the vowels *o* and *u* could not be distinctly formed—the proper tone being injured by the elongation of the pipe necessary to produce them; and this, Mr. Willis remarks, is exactly the case in the Human voice, most singers being unable to pronounce *u* and *o* upon their highest notes. That the function of the glottis is essentially that of giving the pitch and timbre of the vocal sounds, was well shown by a case brought before the Medical Society of London by Dr. Foulis, January 14, 1878. The patient had suffered from disease which had necessitated removal of the larynx, the portion excised extending from the root of the epiglottis to the second ring of the trachea; a large hole remained, through which a tube in two parts, resembling an ordinary tracheotomy tube, was passed upwards and downwards, the lower segment containing a vibrating reed, not unlike an accordion stop, the free extremity being directed downwards. On the insertion of the reed and closure of the throat orifice, the patient read, in an intoning but perfectly intelligible and strong voice, part of the Liturgy, the consonantal variations being as clear as in speech with the healthy organs.

665. The most natural primary division of the Consonants, is into those which require a total stoppage of the breath at the moment previous to their being pronounced, and which, therefore, cannot be prolonged; and those in pronouncing which the interruption is partial, and which can, like the vowel-sounds, be prolonged *ad libitum*. The former have received the designation of *explosive;* and the latter of *continuous*.—In pronouncing the *explosive* consonants, the posterior nares are completely closed, so that the exit of air through the nose is altogether prevented; and the current may be checked in the mouth in three ways — by the approximation of the lips—by the approximation of the point of the tongue to the front of the palate—and by the approximation of the middle of the tongue to the arch of the palate. In the first of these modes we pronounce the letters *b* and *p;* in the second *d* and *t;* in the third, the hard *g* and *k*. The difference between *b*, *d*, and *g*, on the one hand, and *p*, *t*, and *k*,* on the other, seems to depend on this:—that in the former group the approximating surfaces are larger, and the breath is sent through them more strongly at the moment of opening than in the latter. The *continuous* consonants may be again subdivided, according to the degree of freedom with which the air is allowed to make its exit, and the compression which it consequently experiences.—1. The first class includes those in which no passage of air takes place through the nose, and in which the parts of the mouth that produce the sound are nearly approximated together, so that the compression is considerable. This is the case with *v* and *f*, which are produced by approximating the upper incisors to the lower lip, and which stand in nearly the same relation to each other as that which exists between *d* and *t*, or *b* and *p*. The sibilant sounds, *z* and *s*, also stand in a similar relation to each other, they are produced by the passage of air between the point of the tongue and the front of the palate, the teeth being at the same time nearly closed. The simple sound *sh* is formed

* For the sake of proper comparison, this letter should be sounded not as *kay* but *key*.

by narrowing the channel between the dorsum of the tongue and the palate; the former being elevated towards the latter through a considerable part of its length. If, in sounding *s*, we raise the point of the tongue a very little, so as to touch the palate, the sound of *t* is evolved; and in the same manner *d* is produced from *z*. This class also includes the *th;* which, being a perfectly simple sound, ought to be expressed by a single letter, as in Greek, instead of by two, whose combination does not really produce anything like it. For producing this sound, the point of the tongue is applied to the back of the incisors, or to the front of the palate, as in sounding *t*;* but whilst there is complete contact of the tip, the air is allowed to pass out around it.—II. In the second class of continuous consonants, including the letters *m*, *n*, *l*, and *r*, the nostrils are not closed; and the air thus undergoes very little compression, even though the passage of air through the oral cavity is almost or completely checked. In pronouncing *m* and *n*, the breath passes through the nose alone: and the difference of the sound of these two letters must be due to the variation in the form of the cavity of the mouth, which acts by resonance. The letter *m* is a labial, like *b;* but in the former the nasal passage is open, the mouth remaining closed, whilst in the latter the nose is entirely closed, and the sound is formed at the moment of opening the mouth; hence the passage from *m* to *b* is made with great facility. The same correspondence exists between *n* and *t*, or *n* and *g* (the particular part of the tongue approximated to the palate not being of much consequence in the pronunciation of *n*); and hence it is that the transition from *n* to *t*, or from *n* to *g*, is so easy, that the combinations *nt* and *ng* are found abundantly in most languages. The sound of *l* is produced by bringing the tip of the tongue into contact with the palate, and allowing the air to escape around it, at the same time that a vocal tone is generated in the larynx; it differs therefore from *th* in the position at which the obstruction is interposed, as well as in the slight degree of compression of the air which it involves. The sound of the letter *r* depends on the absolute vibration of the point of the tongue, in a narrow current of air forced between the tongue itself and the palate.†—III. The sounds of the third class are scarcely to be termed consonants, since they are merely *aspirations* caused by an increased force of breath. These are *h*, and the gutteral *ch*‡ of most foreign languages (the Greek χ). The first is a simple aspiration; the second an aspiration modified by the elevation of the tongue, causing a slight obstruction to the passage of air, and an increased resonance in the back of the mouth. The sound would become either *g* or *k*, if the tongue, whilst it is being produced, were carried-up to touch the palate.§

666. These distinctions come to be of much importance when we apply ourselves to the treatment of defects of articulation. Great as is the number of muscles employed in the production of definite vocal sounds, the number is much greater for those of articulate language; and the varieties of combination which we are continually forming unconsciously to ourselves, would not be suspected without a minute analysis of the separate actions. Thus, when we utter the explosive sounds, we check the passage of air through the

* Hence it is easy to understand the substitution of *t* or *d*, for the English *th*, by foreigners.

† Donders describes no less than four modes in which the letter *r* can be made. 1, by the lips; 2, by the tongue; 3, by the uvula; and 4, by some part between this and the chordæ vocales. The *r*, as ordinarily but distinctly pronounced, is produced by about thirty vibrations of the tongue in the second. The uvular *r* by from nineteen to twenty-eight.

‡ The English *ch* is merely a combination of *t* with *sh;* thus *chime* might be spelt *tshime*.

§ The general classification proposed by Dr. Marshall Hall has been here adopted, with some modification as to the details.

posterior nares in the very act of articulating the letter; and yet this important movement commonly passes unobserved.—We must regard the power of forming the several articulate sounds which have been adverted to, and their simple combinations, as so far resulting from intuition, that it can in general be more readily acquired by early practice than other actions of the same complexity: but we find that among different Races of Men, there exist tendencies to the production of different sounds, which, though doubtless influenced in great degree by early habit (since we find that children, when first learning to speak, form their habits of vocalization in great degree in accordance with the examples amidst which they are placed), are certainly also dependent in part upon congenital constitution; as we often see in the case of children among ourselves, who grow up with certain peculiarities of pronunciation, not thus derived from imitation, of which they do not seem able to divest themselves.

667. It is in want of power to *combine* the different muscular actions concerned in vocalization, that the defect termed *Stammering* essentially consists. Many theories regarding the nature of this impediment have been proposed; and there can be little doubt that it may be attributed to a great variety of exciting causes. A disordered action of the nervous centres must, however, be regarded as the proximate cause; though this may be (to use the language of Dr. M. Hall) either of *centric* or of *excentric* origin—that is, it may result from a morbid condition of the ganglionic centre, or from an abnormal impression conveyed through its afferent nerves. When of centric origin (and this is probably the most general case), the phenomena of Stammering and Chorea have a close analogy to each other; in fact, stammering is frequently one of the modes in which the disordered condition of the nervous system in Chorea manifests itself.—It is in the pronunciation of the Consonants of the *explosive* class that the stammerer experiences the greatest difficulty. The total interruption to the breath which they occasion, frequently becomes quite spasmodic;* and the whole frame is thrown into the most distressing semi-convulsive movement, until relieved by expiration. In the pronunciation of the *continuous* Consonants of the first class, the stammerer usually prolongs them by a spasmodic continuance of the same action; and there is, in consequence, an impeded, but not a suspended respiration. The same is the case with the *l* and *r* in the second class. In pronouncing the *m* and *n*, on the other hand, as well as the aspirates and vowels, it is sometimes observed that the stammerer prolongs the sound by a full and exhausting expiration. In all these cases, then, it seems as if the muscular sense resulting from each particular combination of actions, became the stimulus to the involuntary prolongation of that state. It is possible that the defect may result, in some instances, from malformation of the parts about the fauces, producing an abnormal stimulus of this kind in some particular positions of the organ; and such cases *may be* really benefited by an operation for the removal of these parts. But the effect of such an operation is certainly exerted in most cases through the *mind* of the patient; the expectation of benefit from it tending to improve his command over the muscles of vocalization, which Emotional excitement always impairs; and the improvement is usually proportional to the confidence which he has been led to feel in the result. The slightest disturbance of the feelings is sufficient in most stammerers to induce a complete perturbation of the vocal powers; the very fear that

* By Dr. Arnott this interruption is represented as taking place in the larynx; that such is not usually the case, the Author believes that a little attention to the ordinary phenomena of voice will satisfactorily prove.

stammering will occur, particularly under circumstances which render it peculiarly annoying, is often sufficient to bring it on in a predisposed subject; and the tendency to consensual imitation sometimes occasions stammering in individuals (especially children) who never show the slightest tendency to it except when they witness the difficulty in others.

668. The method proposed by Dr. Arnott for the prevention of Stammering, consists in the connection of all the words by a vocal intonation, in such a manner that there shall never be an entire stoppage of the breath. It is justly remarked by Müller, however, that although this plan may afford some benefit, it cannot do everything; since the main impediment occurs in the middle of words themselves. One important remedial means, on which too much stress cannot be laid, is to study carefully the mechanism of the articulation of the difficult letters, and to practise their pronunciation repeatedly, slowly, and analytically. The patient would at first do well to practise sentences from which the explosive consonants are omitted; his chief difficulty arising from the spasmodic suspension of the expiratory movement being thus avoided. Having mastered these, he may pass on to others, in which the difficult letters are sparingly introduced; and may finally accustom himself to the use of ordinary language. One of the chief points to be aimed at, is to make the patient feel that he *has* command over his muscles of articulation; and this is best done, by gradually leading him from that which he finds he *can* do, to that which he fears he *cannot*. The fact that stammering people are able to *sing* their words better than to *speak* them, has been usually explained on the supposition that, in singing, the glottis is kept open, so that there is less liability to spasmodic action; if, however, as here maintained, the spasmodic action is not in the larynx, but in the velum palati and the muscles of articulation, the difference must be due to the direction of the attention rather to the muscles of the larynx than to those of the mouth.—One of the most important objects to be aimed at in the treatment of stammering, consists in the prevention of all Emotional disturbance in connection with the act of Speech; and this requires the exercise of the Voluntary power over the direction of the thoughts, in the following modes:—1. To *reduce* mental emotion, by a daily, and even hourly, habit of abstracting the mind from the subject of stammering, both while speaking and at other times. 2. To *avoid exciting* mental emotion by attempting unnecessarily to read or speak, when the individual is conscious that he shall not be able to perform these actions without great distress. 3. To *elude* mental emotion, by taking advantage of any little artifice to escape from stammering, so long as the artifice continues to be a successful one.—Much may frequently be done, also, by constitutional treatment, adapted to improve the general vigour of the nervous system.*

CHAPTER XVII.

OF THE INFLUENCE OF THE NERVOUS SYSTEM ON THE ORGANIC FUNCTIONS.

669. Of the modes in which the Nervous System influences the Organic Functions, a great number have been already considered; for it has been shown to be concerned in providing the mechanical conditions, either immediate or

* See on the subject of "Stammering and its Treatment," a useful pamphlet under this title, by Bacc. Med. Oxon, 1850; and Mr. Bishop's treatise "On Articulate Sounds, and on the Causes and Cure of Impediments of Speech."

remote, under which alone these functions can be performed; so that, when its activity ceases, they cannot be much longer maintained. But the influence of the Nervous System is not alone exerted upon the motor or contractile tissues of the body; for there is good evidence that it has a direct operation upon the molecular changes which constitute the functions of Nutrition, Secretion, &c.; and this view may be admitted to its fullest extent, without our being thereby led to regard the processes in question as *dependent* upon Nervous agency—a doctrine for which there seems no valid foundation. Throughout the animal body, it may be observed that, the more Vegetative the nature of any function, the less is it under the influence of the Nervous System, save where that influence is required to bring it into harmony with functions, sometimes by exciting, sometimes by checking, and sometimes by otherwise modifying them, very much in the way that a rider guides and controls the movements of his horse.—It is evident that this influence must be principally exerted through the *Sympathetic* or *Visceral* system of nerves, since a large proportion of the organs on which it operates are supplied by no other: and hence this apparatus has been commonly designated the 'Nervous system of *organic* life' as distinguishing it from the Cerebro-spinal system, which is the 'Nervous system of *animal* life.' There is, however, no such parallelism betweem them as this designation would imply; for whilst the operations of the Cerebro-spinal system *essentially constitute* the Animal life of the individual, those of the Sympathetic cannot be fairly said to do more than *control* and *direct* those of Nutrition and Secretion.—Nor, on the other hand, is such a view justifiable on histological grounds since the whole of the Invertebrata possess only non-medullated fibres, whilst in the Vertebrata, the fibres of Remak, and the medullated fibres are found commingled both in the mixed nerves supplying the skin and muscles, and in the sympathetic fibres that are distributed to the viscera, though, undoubtedly, a considerable difference exists in the relative proportion of the fibres. We shall now inquire into the structure and relations of the Sympathetic System; and shall then examine the nature of the actions which there seems reason to attribute to it.

670. *Sympathetic Nervous System.*—That collection of scattered but mutually-connected ganglia and nerves, of which this apparatus is made up, may be ranged under the following groups:—1. The isolated ganglia and nerves in immediate connection with the Viscera, which seem to be the chief centres of the system; these form three principal plexuses, the *Cardiac*, the *Solar*, and the *Hypogastric*. 2. The double chain of *Prevertebral* ganglia, with connecting cords, which lies in front of the Vertebral column, and which communicates on the one hand with the Spinal nerves, and on the other with the before-named plexuses. Under this head we should probably rank the minute Cranial ganglia, which are situated in the neighbourhood of the Organs of Sense, and in immediate connection with the branches of the Fifth pair that proceed to them; these are the *ophthalmic*, *otic*, *spheno-palatine*, and *submaxillary* ganglia. 3. The *ganglia on the posterior roots* of the Spinal nerves; under which head we are probably to rank not only the *Gasserian* ganglion of the Fifth pair, but also the ganglia near the roots of the Pneumogastric and Glosso-pharyngeal nerves.—The trunks of the Sympathetic are made up of different orders of fibres; some of these having their central termination in the vesicular matter of the Sympathetic ganglia themselves, whilst others are derived from the Cerebro-spinal system. The former, which are all of the 'gelatinous' kind,* are

* It must be carefully borne in mind, that, although the proper Sympathetic fibres are all 'gelatinous,' yet that the Cerebro-Spinal system contains 'gelatinous' fibres of its own, which are very abundant in some parts. An account of Küttner's and Remak's views on

most abundant in the great Visceral plexuses; but they may be traced from the prevertebral ganglia into the Spinal nerves, part of them proceeding to the ganglia on their posterior roots (whence fibres are given-off that mingle with their spinal fibres), whilst other parts enter the anterior roots and mingle with *their* fibres. On the other hand, the latter, which are of the 'medullated' kind, are derived by the same cords of communication (these being commonly termed the 'roots' of the Sympathetic, but being really commissural bands that bring the two systems into connection) from both roots of the Spinal nerves, and pass through the prevertebral ganglia into the Sympathetic system, without undergoing any ostensible change. Thus it appears that the Cerebro-spinal and Sympathetic systems *interpenetrate* one another; each having its own series of ganglionic centres, and of trunks connected with them; but each system transmitting its fibres into the trunks of the other, so as to be peripherally distributed with their ramifications. Giannuzzi* has made a special study of the rami communicantes of the great sympathetic cord in Mammals by the Wallerian method—that is, by dividing particular roots of the spinal cord, and after the lapse of a certain period examining the rami communicantes microscopically with the object of determining whether any, and if any, what amount of degeneration of the nerve fibres had taken place. The results of his observations are that, with the exception of a few fibres, the fibres of the rami communicantes are entirely derived from the spinal cord, or at least have their nutritive centres in the posterior spinal ganglia, and in the spinal cord. The few exceptional fibres are characterized by their great delicacy and the want of double contours, and pass from the sympathetic ganglia through the rami to the roots of the spinal cord. They may be entirely absent. The number of motor fibres sent by the spinal cord to the Sympathetic is greater than the number of sensory fibres. Giannuzzi has also ascertained that the trophic influence of the spinal cord extends along the nerves derived from the spinal cord after they have traversed a sympathetic ganglion. Arndt† describes the ganglia of the Sympathetic as composed of an apparently homogeneous matrix, through which granules giving off from 2 to 4 fine processes, are distributed. According to Frantzel,‡ the cells of the sympathetic and of the spinal ganglia are invested by a capsule of connective tissue formed by an expansion of the neurilemma of the nerves, which is lined by a layer of pavement epithelium. Beale, Arnold, and others describe a single straight fibre emerging from the nucleus of each sympathetic cell (Figs. 193, 194), and a spiral fibre that appears to be in connection with the surface of the cell, and which, after winding for a few turns round the straight fibre, pursues an opposite direction; such cells must be regarded as bipolar. There is some doubt whether the cells of the spinal ganglia present this structure or not; Schwalbe§ and Courvoisier‖ having only been able to discover one fibre originating from each cell; the cells of these ganglia are therefore unipolar.

671. The connections and distribution of the principal trunks and branches of the Sympathetic system may be concisely stated as follows:—In the cervical portion of the sympathetic, the presence of the following nerve-fibres appears to have been satisfactorily demonstrated.¶ 1. Vaso-motor nerves for the

the structural relations of the prevertebral ganglia, will be found in the "Medico-Chirurgical Review," 1868.

* "Richerche esequite nel gabinetto di Fisiologia della R. Universita di Siena," 1872, p. 51. See also Mayer, "Wien. Akad. Sitz.-ber.," Bd. lxvi. Abth. 3, p. 52.

† Schultze's "Archiv f. Mic. Anat.," Band x. p. 208.

‡ Virchow's "Archiv," 1867, p. 549. § Schultze's "Archiv," Band iv. p. 45.

‖ Ibid., Band ii. p. 13, and Band iv. p. 125.

¶ See Hermann, "Grundriss der Physiologie," 1867, p. 424.

corresponding half of the head, that probably arise from a centre situated in the medulla oblongata, which governs the tone not only of these vessels, but of the entire vascular system throughout the body. This ganglionic centre is constantly in action. Its influence can be abolished by section of the spinal cord in the cervical region, and may be reflectorially depressed, as Cyon and Ludwig have shown, by irritation of the depressor nerve, which is a centripetal branch of the vagus (§ 238). A local depression of its influence may be also reflectorially induced by irritation of the sensory nerve supplying any part* whilst its action may be excited through the agency of carbonic acid. 2. Fibres distributed to the dilatator pupillæ, that probably arise from the oculo-pupillary or cilio-spinal centre, seated in the medulla oblongata—a centre that, like the preceding, is in a constant state of activity, and is influenced in a manner similar to the respiratory and vaso-motor centres; hence in dyspnœa the pupil dilates, and the vessels distributed to the eye contract. 3. Secretory fibres for the salivary glands, irritation of which contracts the vessels and modifies the characters of the secretion, whilst section is followed by dilatation of the vessels. 4. Fibres possessing an accelerating, and others exerting a depressing influence on the heart. The former, according to MM. E. and M. Cyon, emerge by the third branch of the inferior cervical ganglion; whilst the first and second branches constitute the roots of the depressor nerve. 5. Fibres passing to the central cerebro-spinal organs, which reflectorially stimulate the nerves retarding the action of the heart. As regards the thoracic portion of the sympathetic trunk, Otto Nasse† and Bernard only obtained negative results from its division or excitation. The superior thoracic ganglion gives accelerator fibres to the heart. The plexus cardiacus, arising from the thoracic sympathetic, also receives branches from the vagus and the depressor nerves. The splanchnic nerves, which arise from the lower six thoracic ganglia, contain fibres exerting an inhibitory, and others exerting an exciting influence‡ over the movements of the intestine; secretory fibres acting on the kidneys (Bernard); vaso-motor nerves influencing the calibre of the whole abdominal system of vessels;§ and lastly, centripetal fibres exerting reflectorially an inhibitory influence on the action of the heart. The abdominal portion gives off numerous branches which aid in forming the cœliac, mesenteric, renal, suprarenal, spermatic, and hypogastric plexuses, and these, when irritated, occasion movements in the parts to which they are distributed, as the intestine (small and large), bladder, ureters, uterus, vesiculæ seminales, spleen, &c., partly by their direct action on the muscular fibres, partly by modifying the supply of blood to them.‖ Of the *ophthalmic* ganglion (§ 447), the branches are distributed, not merely to the iris, whose radiating fibres are made to contract through their instrumentality, as already explained (§ 567); but also to the vascular apparatus of the eyeball, and especially to the ciliary processes, which seem to possess a sort of erectile character. The *otic* ganglion, which communicates with the third division of the Fifth pair and with the Glosso-pharyngeal, may be considered, from the distribution of most of its branches to the tensor tympani and circumflexus palati muscles, as ministering to the exercise of the sense of Hearing, in somewhat the same mode that the ophthalmic ganglion seems to do to that of vision (§§ 447, 604). The

* Löven, Ludwig's "Arbeiten aus der Physiolog. Anstalt zu Leipzig," 1861, p. 1.

† "Essays on the Physiology of the Movements of the Intestine." Pamphlet, 1866.

‡ Pflüger, Nasse, loc. cit. The splanchnic nerves (Bidder, Reichert and Du Bois-Reymond's "Archiv," 1869, p. 472) in the cat contain three kinds of fibres—viz., 1, Broad medullated fibres, often collected into fasciculi; 2, Slender medullated fibres; 3, Slender Remak's fibres.

§ v. Bezold, Untersuch. passim. Cyon, and Ludwig, "Arbeiten," &c. 1867.

‖ See Nasse, loc. cit.

spheno-palatine ganglion (Fig. 258), whose connections are with the Fifth and the Facial nerves, seems in like manner to minister, by the distribution of its branches on the mucous membrane of the nasal cavity and the palate, to the senses of Smell and Taste. It has been shown by Prévost* to be purely sensory in its function. Of the *submaxillary* ganglion, which also is chiefly connected with the Fifth and the Facial nerves, the branches proceed almost entirely to the Submaxillary gland, and according to Pflüger† and Palladino,‡ terminate in the gland cells. 6. The fibres which arise from the ganglia on the posterior roots of the Spinal nerves (if really belonging to the Sympathetic system) must be distributed along with the branches proceeding from the trunks which they help to form; as must also a part of those fibres which are sent from the proper Sympathetic ganglia into the roots of the same nerves, a large part of them, however, being distributed upon the blood-vessels of the Spinal Cord itself.

672. If, then, it be inquired what inferences we are entitled to draw respecting the functions of the Sympathetic system of nerves, from our knowledge of its Anatomical distribution, we are at once justified in replying that the muscular tissue which directly enters into the formation of the vessels, and especially of the smaller arteries, is supplied essentially from this source. In accordance with this, it is found that excitation of the sympathetic nervous ganglia, whether by direct or reflex irritation, leads to contraction of the vessels, and consequent diminution in the activity of all organic processes, such as secretion, nutrition, growth, and development; their paralysis, as is well seen in cases of section of the cervical sympathetic, disclosing itself by the establishment of the opposite conditions. Again, it is certain that a large proportion of the Muscular apparatus which directly ministers to the Organic functions—that, namely, which surrounds the alimentary canal from the stomach downwards, with the gland-ducts which open into it, and that, also, which forms the walls of the bladder and uterus, of the ureters and Fallopian tubes—*receives no other nervous supply;* and, consequently, that of whatever motor influence these parts may receive from Mental states or from excitation not applied to themselves, this system of nerves must be the channel. The same may be said, too, in regard to that greater portion of the Glandular apparatus, which is exclusively supplied by the Sympathetic nerve, and chiefly by the plexuses that embrace its blood-vessels; since any such alterations in its rate of activity, or in the character of its products, as depend upon conditions of Mind, can be brought about through no other instrumentality.—It is not a little remarkable, however, that those portions of the Muscular apparatus of Organic life, which most obviously exhibit in their action the influence of the Nervous system, both in their respondence to emotional states and in their 'sympathy' with disturbance in other functions—namely, the Heart and the Stomach—derive a considerable part of their nervous supply directly from the Cerebro-spinal system. And it is still more significant that most of those glands whose function is occasional, and whose states of activity are most obviously influenced by affections of the Mind, are specially supplied by Cerebro-spinal nerves, in addition to the Sympathetic plexuses which they receive on the walls of their blood-vessels: thus, the Lachrymal and Salivary glands are supplied with branches of the Fifth and Facial nerves; and the Mammary glands by branches of the Intercostals. It cannot but be deemed highly probable, then, from this circumstance alone, that the influence of mental states upon the function of

* Brown-Séquard's "Archives de Physiologie," tom. i. p. 207.
† Loc. cit. ‡ Abstract in "Centralblatt," 1873, p. 782.

Secretion may be exerted through the nerves of the Cerebro-spinal system, as well as through those of the Sympathetic.

673. It must be in virtue of the connections of the Sympathetic with the Cerebro-spinal system, that the parts which are solely supplied with nerves from the former, are capable of transmitting sensory impressions to the Sensorium. It is true that, under ordinary circumstances, these parts are insensible; that is, impressions made upon them do not travel onwards through the Spinal Cord to the Encephalon: but their sensibility is acutely manifested in morbid states, in which the impressions seem to be propagated further than usual, in virtue of their greater potency. That it is the office of the ganglia on the roots of the Spinal nerves to "cut off sensation," that is, to prevent the further transmission of sensory impressions, is an old doctrine; and there seems much reason to believe that this may be effected by the free communication between one ganglion cell and another, which is established through the vesicular substance of a ganglion, so that the whole force of ordinary impressions on the nerve-fibres is lost by diffusion among the rest of their contents. The same principle seems to apply to the motor fibres; for there are cases which show that when fibres obviously belonging to Cerebro-spinal nerves pass through Sympathetic ganglia, they do not so rapidly or so surely transmit motor impulses, as when they have no such relation to ganglia.*

674. The effects of section and of galvanization of the cut extremities of the sympathetic nerve in the neck have been carefully investigated by Bernard, Waller, Brown-Séquard,† and others. On dividing the nerve, the blood-vessels of that side of the head dilate, and with the freer current of blood which is then established through the capillaries, an increase of the vital properties of all the tissues on the same side of the head is associated. Thus the sensibility of the retina for light appears to be augmented, whence follow contraction of the pupil, retraction of the globe of the eye, partial closure of the eyelid, and projection of the *membrana nictitans* (where present) with increased flow of tears. The temperature and sensibility of the skin, and the cutaneous secretions, are also much increased—the temperature in some of Dr. Waller's experiments‡ rising as much as 18° Fahr., and the skin in some of M. Bernard's being bathed with perspiration. The colour of the venous blood assumes a brighter hue, and its coagulation is more rapid. The muscles respond more readily to weak, and more energetically to strong, stimuli, and retain their irritability longer; rigor mortis consequently sets in more slowly and endures for a longer period; hypertrophy of the facial bones has been noticed by Schiff, and Benedikt§ has observed a similar result to occur in certain muscles; whilst it further appears from Snellen's researches‖ that even the inflammatory and reparative processes, as the effusion of serum, the formation of pus, the absorption of effused blood, and the cicatrization of wounds, take place with very much greater energy than rapidity. On the contrary, when the upper cut extremity of the nerve is galvanized, all these phenomena are reversed: for now, as a consequence of the contraction of the blood-vessels and the diminished supply of blood which ensues, the vital properties of the tissues are diminished, the pupil dilates, the eyelid is widely opened, the temperature and sensibility of the parts decrease, the contractile power of the muscles is less strongly marked, their normal galvanic current is feeble, and cadaveric rigidity sets in quickly and soon passes off, putrefaction

* See Messrs. Kirkes and Paget's "Handbook of Physiology," p. 420.

† See "Lectures on the Central Nervous System," 1860, lectures ix. and x.

‡ "Comptes Rendus," 1853. § "Electro-thérapie," Wien, 1868, p. 88.

‖ Henle and Meissner's "Bericht," 1857, p. 373.

immediately supervening. The effects produced by section of the Sympathetic in the neck are much more strongly marked when the cervical ganglia are destroyed, and Bernard* states that closely similar results follow section of the Sympathetic nerves distributed to the vessels of the extremities. In these later experiments he found that division of the roots of the spinal nerves within the spinal canal, though abolishing sensation and motion in the limb beyond, yet produced no effect upon its temperature; whilst if after such section the sciatic or brachial nerves were divided, an immediate exaltation of temperature ensued; clearly showing that the nerve-fibres devoted to the conduction of sensory and motor impulses issuing from the spinal cord had been joined by a third set of fibres, either proceeding directly from the sympathetic ganglia, or through and beyond these from some part of the cerebro-spinal system, the office of which is to preside over the contraction of the vessels and calorification. A further corroboration of this view was obtained by experiments in which the lumbar ganglia of the Sympathetic were destroyed, when the vascular changes and the increase of temperature in the lower limb were observed without the occurrence of any paralysis. Dr. Waller† has shown that some of the results of irritation of the cervical portion of the sympathetic may be made apparent during life by pressure of the point of the finger behind the ramus of the jaw, though they are associated with other phenomena proceeding from irritation of the pneumogastric. The more important symptoms observed were dyspnœa, cardiac and gastric disturbance, tingling and heat of the ear, lasting for upwards of half an hour, and in one instance dilatation followed by contraction of the pupil. Dr. Waller‡ has also ingeniously shown the effects of paralysis of the vaso-motor nerves of the arm in the living body, by applying a freezing mixture to the ulnar nerve at the elbow; the effect in the first instance being to produce a fall of temperature equal to about 0·5° C. in the two inner fingers; but as the vaso-motor nerves became paralysed, the temperature gradually rose till it attained a height of from 5° to 6° C. above that of the outer fingers: the difference between the outer and inner fingers appeared to be partially attributable to a decrease in the temperature of the former as well as to an increase in that of the latter, owing to the diversion of part of the blood of the radial into the ulnar artery. The effects of percutaneous excitation of the sympathetics in man by means of electricity are very slight, consisting only, according to MM. Eulenberg and Guttmann,§ of an almost inappreciable dilatation of the pupil, and a lowering of the frequency of the pulse. As the smaller vessels contract, there is probably an increase of pressure in the larger ones, but it must be remembered that it is difficult to irritate the cervical Sympathetic without coincidentally exciting the vagus-depressor nerve of Cyon, the laryngeal nerve, and descendens noni, which may materially influence the result. The vaso-motor nerves of the upper extremity do not proceed from the spinal cord, in common with the sensori-motor nerves forming the brachial plexus, but issue from it at a much lower point—namely, between the third and seventh dorsal nerves. The vaso-motor nerves for the lower extremities spring from the adjoining dorsal roots, and not from those which form the sciatic plexus. The chief vaso-motor of the body which supplies all the vessels distributed to the viscera is the splanchnic nerve, and by reason of the large quantity of blood these vessels can contain the splanchnic nerve plays the principal part in the distribution of the blood

* See "Gazette Hebdomad.," Août, 1862; "Comptes Rendus," vol. ii. 1862; and "Journal de la Physiologie," vol. v.

† "Proceedings of the Royal Society," vol. xi. p. 302. ‡ Ibid. p. 436.

§ "Die Pathologie des Sympatheticus," 1873, p. 202.

generally in the body.* If it be irritated, the blood is driven in large quantity into the vessels of the head and limbs, whilst if it be paralysed the blood accumulates in the viscera, and the head and extremities are rendered anæmic. Budge† maintains that the small arteries throughout the body can be made to contract by electrical irritation of the pedunculus cerebri, which, therefore, he regards as the centre of the vaso-motor nerves, but there can now be no question that the principal vaso-motor centre is, as already stated (§ 238), situated in the medulla oblongata.

675. It is very difficult to give a satisfactory explanation of the *dilatation* observed in the vessels of certain regions of the body when the nerves supplying them are irritated. The most marked instances of such dilatation are seen in the vessels of the submaxillary gland when the chorda tympani, and in those of the penis when the nervi erigentes are stimulated. In the latter case, if the nerves of both sides be cut, erection of the penis on sexual excitement or by mechanical irritation of the sensory fibres in the pudendal nerves is rendered impossible ; yet if the distal extremities of the nerves be irritated, the corpora cavernosa swell, and the copious flow of bright-coloured blood that follows an incision into them, shows that the circulation has been greatly increased in activity. Claude Bernard‡ and Schiff § admit a direct dilating action of the nerves, and this view receives support from the experiments of Mr. Gaskell.‖ Others have suggested that in the case of the penis the phenomena are due to the contraction of the small veins, or to contraction of the trabeculæ of the corpora cavernosa impeding the return of blood ; but against this it has been shown that erection does not follow ligature of the principal veins. M. Legros,¶ again, believes that they are due to an exaggeration of the ordinary peristaltic action of the smaller arteries, but it is not easy to understand how this could act in the absence of valves. It is not improbable that two conditions co-operate in producing the increased flow of blood in the instances adduced above. On the one hand, as is especially seen in the case of the submaxillary gland, irritation of the chorda tympani may augment the attraction of the tissue of the gland for the blood, and thus act in producing a *vis a fronte*, and on the other, as occurs more particularly in the case of the penis, the nervi erigentes exert, when stimulated, an inhibitory influence over the ordinary vaso-motor and constricting nerves exactly comparable to that of the vagi over the movements of the heart. *Reflex* dilatation of vessels has

* See Cyon, "Electrothérapie," 1873, p. 203.

† Pflüger's "Archiv," Band vi. 1872, p. 303.

‡ C. Bernard, "Leçons sur les Liquides de l'Organisme," t. i. p. 230; and "Révue Scientifique," 1872, p. 119.

§ M. Schiff, "De l'Inflammation," 1873.

‖ "Journ. of Anat. and Physiol.," vol. xi. 1877, pp. 393 and 720. See also Foster's "Journal of Physiology," vol. i. pp. 108 and 262. This observer finds in the case of the mylo-hyoid muscle of the frog in which the changes in diameter of the vessels on stimulation of the nerve supplying the muscle, may readily be followed, that there is a latent period lasting five or six seconds, and not preceded by constriction (so that there was no question of exhaustion). This was followed by dilatation which reached its maximum in from 20 to 30 seconds, and then gradually subsided till the stream became normal. The dilatation was in some instances so great that the diameter of the artery increased to nearly three times the size it possessed before the commencement of the stimulation. Curare, when administered to an animal, affects the dilator fibres alone, and not the constrictor.

¶ Ch. Legros, "Des Nerfs Vasomoteurs," Thèse, Paris, 1873, p. 67. For other papers bearing on this subject, see Eckhard, "Beiträge zur Anatomie," Abhand. vii. 1863; Lovén, Ludwig's "Arbeiten," 1866, p. 1; Kölliker, "Würzburger Verhandlungen," Band ii.; Goltz, Pflüger's "Archiv," 1873, p. 346; Brown-Séquard, "Leçons sur les Nerfs Vasomoteurs," pp. 25–65; v. Wittich, Virchow's "Archiv," 1866, Band xxxvii. p. 93; Heidenhain, Pflüger's "Archiv," Band v. p. 40; Vulpian, "L'Appareil Vasomoteur," 1875, p. 160.

been observed by Lovén,* who found that when the central ends of the saphena and great auricular nerves were stimulated in the rabbit dilatation of the saphena artery and of the median vein of the ear respectively occurred, and the effects of stimulation of the branches of the Fifth nerve distributed to the tongue on the vessels of the salivary glands has been already alluded to.

676. It can only be through the Nervous System that the Muscular apparatus of Organic life is acted upon by states of Mind. Although no exertion of the *Will* can produce an effect upon any part of it, yet there are various organs whose muscular walls are influenced on the one hand by Emotional states, and on the other by the state of Expectant Attention. The Heart sympathizes so much with the Emotions, that the language of almost all civilized nations refers to it as the *seat* of the 'feelings'; but we have as yet no certain evidence whether this influence is transmitted through the Sympathetic or through the Pneumogastric nerve. The former seems the more probable channel, when we bear in mind that it can be through the sympathetic alone that those alterations in the diameter of the blood-vessels take place which give rise to the *blush* of modesty or shame, or to the pallor which alternates with this in many states of mental agitation.† So, again, the influence of Emotional states is strikingly manifested in the production of the peculiar turgescence of the Erectile tissues (§ 257); and here we have a striking example of the utter powerlessness of the Will in the well-known fact, that no amount of sexual *desire* will produce erection, if the mind be possessed with any feeling of doubt or apprehension as to the existence of the sexual *ability*. The muscular walls of the alimentary canal seem frequently to be excited to increased action by agitating emotions; but it may be doubted how far this is a primary effect of the mental state, or how far it is consequent upon the influence of that state upon the secretions poured into the Canal.—The influence of the state of *expectant attention*, as of the emotions, is strongly manifested in the case of the Heart; the action of which, as Sir H. Holland has remarked, "is often quickened or otherwise disturbed by the mere centering the consciousness upon it, without any emotion or anxiety. On occasions where its beats are audible, observation will give proof of this, or the physician can very often infer it while feeling the pulse; and where there is liability to irregular pulsation, such action is seemingly brought on, or increased, by the effort of attention, even though no obvious emotion be present."‡ There can be no doubt that the movements of the lower part of the Alimentary Canal are capable of being affected in a similar manner; since we may frequently trace the rapid descent of the fæcal mass into the rectum, when we expect to be shortly able to discharge it; and it is in great part in this mode, that *habit* operates in producing a readiness for defecation at particular times, and that bread-pills and other supposititious purgatives unload the bowels."§

* Ludwig's "Arbeiten," 1866.

† The pallor of extreme fear or terror is probably due rather to a state tending to Syncope, arising from a partial failure of the heart's action.

‡ "Chapters on Mental Physiology," p. 16.

§ The Author may mention the two following cases, which have fallen within his own knowledge, as curious illustrations of the influence of mental states upon the movements of the alimentary canal.—The first of these occurred in the person of a literary man, of a somewhat hypochondriacal temperament, who had been troubled with continued costiveness, for which he had been accustomed to take an aperient pill daily. Finding that this ceased to have its usual effect, and being fearful of increasing his regular dose, he applied for advice to a practitioner, who, having had former experience of what Mental agency alone would do, determined to try its effect in this instance. Seating his patient before him, with the abdomen uncovered, he desired him to fix his attention intently upon his abdominal sensations, and assured him that in a short time he was quite certain that he would begin to feel a movement in his bowels, which would end in a copious evacuation. He himself did nothing but

677. *Trophic Nerves.*—The existence of a special system of nerves possessing a direct influence on the process of nutrition, though suggested by other writers, was first clearly enunciated by Samuel of Leipsic, and has been so warmly supported by Duchenne, that he has declared that "if trophic nerves did not exist, it would be necessary to invent them." The positive facts which have led to their admission are, however, comparatively few, and in fact may almost be considered as limited to the single one, demonstrated by Ludwig, that certain glands can be excited to action by the stimulation of their nerves, independently of their blood supply (§ 107). The view taken by Samuel* is that the so-called trophic nerves arise from the ganglia on the posterior roots of the spinal nerves and run centrifugally to the tissues. When stimulated increased activity of all the nutritive processes is observed, cell-growth in particular taking place with abnormal rapidity. On the contrary, their paralysis, as by section, leads to diminished activity in the nutritive operations, and atrophy. In proof of these statements Samuel adduced the results of many experiments showing that if a rough fragment of bone be passed beneath the sciatic nerve stretching it like a cord and producing continual irritation of its fibres, the thigh, leg, and foot swell in the course of 24 or 36 hours. The whole limb below the seat of irritation of the nerve becomes hyperæsthetic, its temperature rises, and an ill-smelling discharge takes place from the wound, all circumstances indicating the increased activity of the various processes both of nutrition and disintegration. In like manner laryngitis may be produced by irritating the superior laryngeal nerves, and after death the mucous membrane is found swollen and reddened; so by irritation of the Vagi, just below their exit from the skull, the symptoms and pathological conditions characterizing pneumonia may be obtained, and by irritating the spinal cord with a bristle dipped in croton oil passed through it in such a direction as to affect the posterior roots of the spinal nerves at the level of the last dorsal vertebra, he observed great hyperæmia, tumefaction, and elevation of temperature in the lower limbs.† Dr. Axmann found that when the spinal nerves of frogs were divided on the distal side of their prevertebral ganglia, the nutrition of the parts supplied by them was much more injuriously affected than it was when the section was made between the ganglia and the spinal cord. A large number of pathological cases are on record which certainly appear to support the views of Samuel. One of the most typical is that given by Sir James Paget in his lectures on Nutrition, on the authority of Mr. Hilton:—"A man was at Guy's Hospital, several years ago, who, in consequence of fracture of the lower end of the radius, repaired by an excessive quantity of new bone, suffered compression of the median nerve. He had ulceration of the thumb, and of the fore and middle fingers, which had

look steadily at his patient, with an air of great determination and confidence, and point his finger at the abdomen, moving it along the arch of the colon, and (as it were) in the course of the convolutions of the small intestines, so as to aid the patient in fixing his attention upon them. In a short time the expected movements were felt, and a copious evacuation soon followed; and for some time afterwards the bowels continued to act freely without medicine.—In the other case, a Lecturer at a public Institution was seized with a strong impulse to defecate during his lecture; and was greatly inconvenienced by the effort necessary to restrain it. Before every subsequent lecture in the same place, the same impulse returned upon him, notwithstanding that he might have previously unloaded his bowels elsewhere. In this case, there was obviously a state of apprehension combined with the simple anticipation; but the influence of the latter is shown by the fact, that in no other place did this individual experience the impulse in question under the like circumstances.

* "Die trophische Nerven," 1860.

† See also for corroborative experiments, Laborde and Leven, "Gaz. Médicale," 1870; Vulpian, Brown-Séquard's "Archives," 1872, p. 384.

resisted various treatment, and was cured only by so binding the wrist, that the parts on the palmar aspect being relaxed, the pressure on the nerve was removed. So long as this was done, the ulcers became and remained well; but as soon as the man was allowed to use his hand, the pressure on the nerves was removed, and the ulceration in the parts supplied by it returned."* In the American war a special Hospital having been set aside for injuries and diseases of nerves, the surgeons, Messrs. Mitchell, Morehouse, and Keen, had large opportunities of observing the effects of such lesions. The conditions they found to occur in the parts below the seat of injury were atrophy of muscles, and various subacute inflammatory states indicated by tumefaction and congestion, œdema, thickening of the cuticle and glossiness of the skin, cracks and fissures in it, bed-sores, eczema, curved and talon-like nails, retraction of the skin of the ungual phalanx and exposure of the matrix, painful swelling of joints and altered or arrested secretions (Sweat). Bärensprung again has satisfactorily shown that in some cases of Herpes, at least, the ganglia on the posterior roots of the spinal nerves are inflamed, and Vandyke Carter† has pointed out that in cases of leprosy the cutaneous affection is often limited to certain nerve-regions, which become anæsthetic, whilst post-mortem examination shows that the nerves in question are swollen and affected with hypertrophy of the interstitial connective tissue. Lesions of the spinal cord and hemiplegia of cerebral origin are often rapidly followed by disease of the joints (Charcot), and lesions of certain parts of the encephalon, as the optic thalamus, corpus striatum, and pons, are followed by ecchymosis of the lungs, pleura, and stomach. Looking at the facts obtained from clinical observation, Hermann thinks it is legitimate to conclude, not that the existence of trophic nerves is satisfactorily established, but that the central grey matter of the nerve centre, the nerve fibre, and the peripheric terminal organ, represent not only a functionally active body, but a trophic or nutritive unity; so that in the case of muscle or gland, the nerve centre, nerve, and muscular and glandular tissues form one whole, in which various changes take place, the last expression of which is in the muscle contraction and in the gland secretion, and the central and peripheral extremities of the nerve mutually reacting on one another. The arguments for and against the existence of *trophic nerves* are numerous and of nearly equal weight, so that it is difficult in the present state of knowledge to make a positive statement in regard to them. As Hermann,‡ who has stated these arguments most clearly, remarks, much of the evidence in favour of their existence has been drawn from clinical observations and not from physiological researches, though the former method of inquiry has many disadvantages. The first observations that led to the suggestion of the presence of a distinct set of trophic nerves were those of Magendie, who showed that, after intra-cranial section of the fifth pair of nerves of one side, the eye of the same side was apt to become inflamed; the cornea first became cloudy, then losing its epithelium, and the deeper tissues being successively invaded, till suppuration of the globe followed by atrophy occurred. These changes were regarded as the effects of the division of trophic nerves. Disturbances in the nutrition of the mucous membrane of the lips, after intra-cranial division of the fifth nerve, were also noticed by

* Similar cases are given by M. Gillette in the "Dictionnaire Encyclopédique," by M. Charcot in Brown-Séquard's "Archives de Physiologie," and Mr. I'Anson, "Lancet," 1871, vol. ii. p. 913; by Hutchinson in the "London Hospital Reports" for 1866; by Schiefferdecker and Edis, a storehouse of such facts in the work of Messrs. Mitchell, Morehouse, and Keen, "On Gunshot Wounds and other Injuries of Nerves."

† "British and For. Med.-Chir. Rev.," 1863, January.

‡ "Handbuch der Physiologie," Band i. 1879.

Bernard and others. Division of both vagi in the neck is followed by serious disturbance of the functions of the lungs and other organs, which ultimately occasion death. Section of the sciatic nerve leads, in many instances, to ulceration of the foot. Schiff,* again, has shown that after section of all the nerves proceeding to an extremity, the limb diminished in size, the periosteum became thickened and lamellated, and the inorganic constituents of the bones appeared to have diminished. Similarly, Obolensky,† after practising division of the nerves in the cord supplying the testes, found that on the side of the lesion the testes in the course of four months became atrophied, and the contents of the tubulus had undergone fatty degeneration. After section of the vas deferens alone, without injury of the nerves, the testes long preserved their normal characters. The effects of division of the nerves supplying the submaxillary gland in the dog‡ are diminution in the volume, weight, and consistence of the gland, and a change in its colour from yellow to reddish-grey. Extirpation of the upper cervical ganglion in young cocks§ is followed by atrophy of the comb. Division of the cervical sympathetic in rabbits is said to cause increase in the growth of the ears and more rapid growth of the hair on the injured side; whilst division of the nerves of both sides is followed by diminution in the volume of the brain, after eighteen months, as compared with a similar and uninjured animal.‖ Section of motor nerves leads to atrophy, and even disappearance of the proper muscular tissue, proliferation of the nuclei, and development of connective tissue. On the other hand, it must be acknowledged that many of the phenomena above noticed, and which have been held to demonstrate the existence of trophic nerves, admit of another explanation. Thus, in the case of the lesions of the eye and of the mucous membrane of the mouth, occurring after division of the Fifth nerve, there is strong reason for believing that they are due to the loss of sensibility of the parts, which permits foreign and irritating substances to remain long in contact with the parts first affected, and precludes the performance of those protective movements which, under ordinary circumstances, are employed to prevent mischief. The entry of particles of dust into the eye, and the lodgment of particles of food between the cheeks and teeth, constitute sources of irritation that are commonly removed by winking, rubbing the eyes with the fingers or in animals with the fore-foot, a flood of tears, or by the movements of the tongue; but if allowed to remain, inflammation, proceeding to ulceration, soon occurs; and the best evidence that this is really the cause of the damaged eye is the fact, that if the eye be protected with a watch-glass, the inflammatory symptoms do not supervene, or, if they have already commenced, rapidly disappear. Again, many of the phenomena regarded as due to lesion of nerves, such as hypertrophy or atrophy of various organs, may with equal probability be referred to the influence of the divided nerves on the vessels, causing increased or diminished blood supply to the part. Where both sides are placed under precisely similar conditions little alteration is noticeable. Thus, Joseph¶ found that if the nerves of one extremity were divided, and both were then embedded in plaster of Paris, no changes enabling

* Schiff, "Comptes Rendus," 1854, p. 1050; Kassowitz, "Centralblatt f. d. Med. Wiss.," 1878, p. 790; Vulpian, "Leçons," 1875, p. 352.

† "Centralblatt f. d. Med. Wiss.," 1867, p. 497.

‡ See Bernard, "Journal de l'Anat.," 1864, t. i. p. 507; Bidder, "Archiv f. Anat. u. Physiologie," 1867, p. 25; Heidenhain, "Studien des Physiol. Institut. zu Breslau," iv. 1868, p. 77.

§ See Legros, "Des Nerfs Vasomoteurs," Paris, 1873.

‖ Brown-Séquard, "Comptes Rend. de la Soc. de Biologie," 1872, p. 194.

¶ "Centralblatt f. d. Med. Wiss.," 1871, p. 721; and "Archiv f. Anat. u. Physiol.," 1872, p. 206.

him to determine which was the injured side were perceptible. Brown-Séquard and others have in like manner found very few and slight trophic changes after division of one cervical sympathetic. Then, again, there are the remarkable phenomena observed and described by Snellen, Schiff, and many others,* which follow intra-cranial section of the fifth pair of nerves, and which consist in the occurrence of conjunctivitis within a few hours of the operation, the discharge of a thick, puriform mucus, haziness, ulceration, and ultimately sloughing of the cornea, and the loss of the eye on the same side as that on which the nerve has been divided. Lastly, there are the atrophic changes which occur in muscles when a motor nerve is divided, and which have been described with great minuteness by M. Vulpian,† by Erb, and others, the fibres losing their transverse striæ, and gradually undergoing fatty degeneration, whilst the nuclei of the sarcolemma and the interstitial connective tissue undergo hypertrophy. Thus it would at first sight appear there is a large amount of evidence proving the direct influence of the nervous system on the processes of nutrition.

678. It is not less certain, however, that weighty evidence can be adduced to show that the nervous system is not required for the due performance of the nutritive processes, and has little or no direct action upon them, the pathological phenomena above mentioned as concurrent with their persistent irritation, or consequent on their paralysis, resulting from changes in the supply of blood, which again are caused by the action of the vaso-motor nerves upon the vessels. In proof of this it may be observed, in the first place, that nutrition and the processes which minister to it, as absorption, assimilation, circulation, secretion, the fixation of new material, and the disintegration and removal of the old, are all actively performed by plants, though there is no evidence of the existence of such a rudimentary nervous system in the vegetable kingdom. Again, in many of the lower forms of animal life, as well as in the more lowly organized tissues of the higher animals, such as cartilage, fat, and connective tissue, few or no nerves are present, and nervous influence, if perceptible at all upon the process of nutrition in them, must therefore be indirect. Thirdly, daily experience shows that even in the higher animals, sensory nerves may be divided without any failure in the processes of nutrition of the parts they supplied.‡ In regard to *motor* nerves, the experiments of Reid made long ago showed clearly that although atrophy of muscle follows section if the limb be allowed to remain quiescent, yet that the muscles retain all their characters if they are methodically exercised by passive movement, or by the action of the electrical current. Brown-Séquard records cases where *mixed* nerves§ have been divided without apparent alteration being produced either in the temperature or in the nutrition of the parts beyond. Lastly, even with regard to the sympathetic there is evidence that section of its trunk on one side in the neck, if anything, improves rather than deteriorates nutrition on the same side of the head, for the vaso-motor system being paralysed, the current of blood becomes freer, causing the hair on that side to grow more rapidly in the mammal, and the lateral half of the comb of the cock to hypertrophy, whilst injuries heal more rapidly and the tissues, as in the case of the cornea especially, are more tolerant of irritation and injury ; and such cases as those recorded by Dr. Carnochan and Dr. Conner‖ where Meckel's

* See especially Sinitzin, "Centralblatt für die Med. Wiss.," 1871, p. 160.

† Brown-Séquard's "Archives," 1872, p. 753.

‡ See case by Vanzetti (Brown-Séquard's "Archives," 1872, p. 152), in which the lingual nerve was resected on one side, and in three months after the organ still preserved its normal form, colour, and nutrition.

§ "Archives," 1869.

‖ "Amer. Journ. of Med. Sci.," October, 1870, and "New York Med. Journ.," No. 69, p. 579.

ganglion was extirpated, and no apparent mischief followed, show that some other conditions than the mere abolition of the function of the sympathetic ganglia must be present in order that impairment of nutrition may take place.

679. It is to be observed, moreover, that whilst some of the phenomena above alluded to are explicable on the supposition that the blood-supply is interfered with, possibly by persistent contraction of the blood-vessels, in others there may have been some interference with the lymphatic system, the relations of which to the nerves is at present unknown, whilst others again admit of a different explanation. Take, for example, the case of the eye after division of the fifth nerve. The experiments of Büttner and Meissner,* v. Bezold,† v. Hippel, and others have shown that if the eye be carefully covered and protected from external lesion, no pathological lesions occur after the section, whilst if it be exposed ulceration soon sets in. Here it is probable that the loss of sensibility of the cornea leads to dryness, and the entrance of foreign bodies, in consequence of the ordinary act of winking being neglected, and such dryness is a predisposing cause to inflammation. In a case under the care of the Editor, in which the fifth nerve was paralyzed on both sides, one eye was wholly lost, but in the other incomplete ptosis occurred, and the inflammation was long limited to the part of the cornea exposed in the half-shut condition. In this part a deep ulcer formed, whilst the rest of the cornea was perfectly bright and transparent, and the iris was not implicated till a very late period. In like manner Brown-Séquard has shown that many of the effects which may be observed to follow injuries of the nerves of the extremities, may be referred to a want of power on the part of the animal, both to perceive and to withdraw them from irritating and depressing conditions (cold, wet, and pressure). It must be remembered also that many of Mitchell's cases were severe gunshot wounds, and that the blood-vessels and other tissues besides the nerves were always implicated.‡

680. The influence of particular conditions of the Mind, in exciting suspending, or modifying various Secretions, is a matter of daily experience. The *Lachrymal* secretion, for example, which is continually being formed to a small extent for the purpose of bathing the surface of the eye, is poured out in great abundance under the moderate excitement of the emotions, either of joy, tenderness, or grief. It is checked, however, by violent emotions; hence, in intense grief, the tears do not flow; and it is a well-known indication of moderated sorrow when the gush takes place, this very act affording a further relief. The flow of *Saliva*, again, is stimulated by the sight, the smell, the taste, or even by the *thought* of food, especially of such as is of a savoury character. On the other hand, violent emotion may suspend the salivary secretion; as is shown by the well-known test, often resorted to in India, for the discovery of a thief amongst the servants of a family,—that of compelling all the parties to hold a certain quantity of rice in the mouth during a few minutes,—the offender being generally distinguished by the comparative dryness of his mouthful at the end of the experiment. There is much reason to believe that the secretion of *Gastric* fluid is effected, in the same manner as that of the saliva, by the impressions made by food upon the senses; for it has been ascertained by Bidder and Schmidt§ that it is copiously effused into the stomachs of dogs that

* "Berich. üb. die Fortsch. d. Phys.," 1862, p. 412. † "Deutsche Klinik," 1867.

‡ Ludwig and Hafiz, "Arbeiten," 1870; "Practitioner," x. 1873, p. 146. See also Herman Schulz, 'Ueber den Einfluss der Nervendurchschneidung auf Ernährung' "Centralblatt f. d. Med. Wiss.," 1873, p. 708; Joseph, Reichert's "Archiv," 1872, No. 2; Fischer, "Journ. of Anat. and Physiology," vol. vi. p. 222; Vulpian, "Comptes Rendus," 1872, t. lxx. No. 15. § Op. cit. p. 35.

have been kept fasting, when flesh or any other attractive food is placed before them. That the secretion, on the other hand, is entirely suspended by powerful mental emotion, seems almost certain, from the well-known influence which this has in dissipating the appetite for food, and in suspending the digestive process when in active operation. As a cheerful state of feeling, on the other hand, seems to be decidedly favourable to the performance of the digestive function, it probably exerts a beneficial influence, as to both quantity and quality, on the secretion of gastric fluid. Of the influence of mental states on other secretions concerned in the reduction and appropriation of the food (such as the Biliary, Pancreatic, and intestinal fluids), neither observation nor experiment has as yet afforded any satisfactory information. It is a prevalent, and perhaps not an ill-founded opinion, that melancholy and jealousy have a tendency to increase the quantity, and to vitiate the quality, of the *Biliary* fluid. Perhaps the disorder of the organic functions is more commonly the source of the former emotion than its consequence; but it is certain that the indulgence of these feelings produces a decidedly morbific effect by disordering the digestive processes, and thus reacts upon the nervous system by impairing its healthy nutrition. A copious secretion of *fœtid gas* not unfrequently takes place in the intestinal canal, under the influence of any disturbing emotion; or the usual *fluid secretions* from its walls are similarly disordered. The tendency to Defecation which is commonly excited under such circumstances is not, therefore, due simply to the relaxation of the sphincter ani (as commonly supposed); but it is partly dependent on the unusually stimulating character of the fæces themselves. The same may be said of the tendency to Micturition, which is experienced under similar conditions; the change in the character of the *urine* becoming perceptible enough among many animals, in which it acquires a powerfully disagreeable odour under the influence of fear, and thus answers the purpose which is effected in others by a peculiar secretion. The *halitus from the Lungs* is sometimes almost instantaneously affected by bad news, so as to produce fœtid breath. The *odoriferous secretion of the Skin*, which is much more powerful in some individuals than others, is increased under the influence of certain mental emotions (as fear or bashfulness), and commonly also by sexual desire. It appears from the observations of Vulpian, Luchsinger (§ 377), and others to be excreted under the influence of two antagonistic nerve centres, one of which excites, whilst the other inhibits it. The excito-secretory nerves arise in the region of the medulla oblongata, and descending issue from the lumbar region of the Cord, and run in the sciatic nerve. The inhibitory nerves arise also from the medulla oblongata, but enter the sympathetic system of nerves. The *Sexual* secretions themselves are strongly influenced by the condition of the mind. When it is frequently and strongly directed towards objects of passion, these secretions are increased in amount, to a degree which may cause them to be a very injurious drain on the powers of the system. On the other hand, the active employment of the mental and bodily powers on other objects, has a tendency to render less active, or even to check altogether, the processes by which they are elaborated.*

* This is a simple physiological fact, but of high Moral application. The Author would say to those of his younger readers, who urge the wants of Nature as an excuse for the illicit gratification of the sexual passion, "Try the effects of *close mental application* to some of those ennobling pursuits to which your profession introduces you, in combination with *vigorous bodily exercise* (for the effects of which see § 555), before you assert that the appetite is unrestrainable, and act upon that assertion." Nothing tends so much to increase the desire as the continual direction of the mind towards the objects of its gratification, especially under the favouring influence of sedentary habits; whilst nothing so effectually represses it as the

681. No Secretion so strongly manifests the influence of the Nervous system, and especially of Emotional states, both upon its quantity and its quality, as that of the *Mammary* glands. Although the production of Milk, when once established, continually goes on in the breasts of a nursing female, yet it is obviously accelerated in the first instance, and augmented afterwards, by the mechanical irritation of the nipple produced by the suction of the infant; and this alone (or in combination with the strong *desire* to furnish milk) has been effectual in producing the secretion in girls and old women, and even in men. Again, in the nursing female the secretion is often suddenly augmented by the *sight* of the infant, or even by the *thought* of him in absence, especially when associated with the idea of suckling; this gives rise to the sudden rush of blood to the gland, which is known by nurses as the *draught*, and which may probably be attributed to a dilatation of the Mammary arteries, through the instrumentality of their Sympathetic nerves, analogous to that which takes place in the act of blushing (§ 676).—Although we are continually witnessing indications of the powerful influence of Emotional states upon the qualities of the Mammary secretion, yet it is probable that such influence is not at all peculiar to the milk; and that we only recognize it more readily in this case, because the digestive system of the infant is a more delicate apparatus for testing it than any which the Chemist can devise; affording proof, by disorder of its function, of changes in the character of the secretion which no examination of its physical properties could detect. The following remarks on this subject are abridged from Sir A. Cooper's valuable work on the Breast:—"The secretion of milk proceeds best in a *tranquil state of mind*, and with a cheerful temper; then the milk is regularly abundant, and agrees well with the child. On the contrary, a *fretful temper* lessens the quantity of milk, makes it thin and serous, and causes it to disturb the child's bowels, producing intestinal fever and much griping. *Fits of anger* produce a very irritating milk, followed by griping in the infant, with green stools. *Grief* has a great influence on lactation, and consequently upon the child. The loss of a near and dear relation, or a change of fortune, will often so much diminish the secretion of milk, as to render adventitious aid necessary for the support of the child. *Anxiety of mind* diminishes the quantity, and alters the quality, of the milk. The reception of a letter which leaves the mind in anxious suspense lessens the draught, and the breast becomes empty. If the child be ill, and the mother is anxious respecting it, she complains to her medical attendant that she has little milk, and that her infant is griped and has frequent green and frothy motions. *Fear* has a powerful influence on the secretion of milk. I am informed by a medical man who practises much among the poor, that the apprehension of the brutal conduct of a drunken husband will put a stop for a time to the secretion of milk. When this happens, the breast feels knotted and hard, flaccid from the absence of milk, and that which is secreted is highly irritating; whilst some time elapses before a healthy secretion returns. *Terror*, which is sudden and great fear, instantly stops this secretion."

determinate exercise of the mental faculties upon other objects, and the expenditure of nervous energy in other channels.—There seems to be something in the process of training young men for the Medical Profession, which encourages in them a laxity of thought and expression on these matters, that too frequently ends in a laxity of principle and of action. It might have been expected that those who are so continually witnessing the melancholy consequences of the violation of the Divine Law in this particular, would be the last to break it themselves; but this is unfortunately very far from being the case. The Author regrets being obliged further to remark, that some works which have issued from the Medical press contain much that is calculated to excite, rather than to repress, the propensity; and that the advice sometimes given by practitioners to their patients is immoral as well as unscientific.

Of this two striking instances, in which the secretion, although previously abundant, was completely arrested by this emotion, are detailed by Sir A. Cooper. "Those passions which are generally sources of pleasure, and which, when moderately indulged, are conducive to health, will, when carried to excess, alter, and even entirely check, the secretion of milk."

682. There is even evidence that the Mammary secretion may acquire an actually *poisonous* character, under the influence of violent mental excitement; for certain phenomena which might otherwise be regarded in no other light than as simple coincidences, appear to justify this inference, when interpreted by the less striking but equally decisive facts already mentioned. "A carpenter fell into a quarrel with a soldier billeted in his house, and was set upon by the latter with his drawn sword. The wife of the carpenter at first trembled from fear and terror, and then suddenly threw herself furiously between the combatants, wrested the sword from the soldier's hand, broke it in pieces, and threw it away. During the tumult, some neighbours came in and separated the men. While in this state of strong excitement, the mother took up her child from the cradle, where it lay playing, and in the most perfect health, never having had a moment's illness; she gave it the breast, and in so doing sealed its fate. In a few minutes the infant left off sucking, became restless, panted, and sank dead upon its mother's bosom. The physician who was instantly called in found the child lying in the cradle, as if asleep, and with its features undisturbed; but all his resources were fruitless. It was irrecoverably gone."* In this interesting case, the milk must have undergone a change which gave it a powerful sedative action upon the susceptible nervous system of the infant.—The following, which occurred within the Author's own knowledge, is perhaps equally valuable to the Physiologist, as an example of the similarly fatal influence of undue emotion of a different character; and both should serve as a salutary warning to mothers, not to indulge either in the exciting or in the depressing passions. A lady having several children, of which none had manifested any particular tendency to cerebral disease, and of which the youngest was a healthy infant a few months old, heard of the death (from acute hydrocephalus) of the infant child of a friend residing at a distance, with whom she had been on terms of close intimacy, and whose family had increased almost contemporaneously with her own. The circumstance naturally made a strong impression on her mind; and she dwelt upon it the more, perhaps, as she happened, at that period, to be separated from the rest of her family, and to be much alone with her babe. One morning, shortly after having nursed it, she laid the infant in its cradle, asleep and apparently in perfect health; her attention was shortly attracted to it by a noise; and on going to the cradle, she found her infant in a convulsion, which lasted a few moments and then left it dead. Now, although the influence of the mental emotion is less unequivocally displayed in this case than in the last, it can scarcely be a matter of doubt; since it is

* Dr. Von Ammon, in his treatise "Die ersten Mutterpflichten und die erste Kindespflege," quoted in Dr. A. Combe's excellent little work on "The Management of Infancy."—Similar facts are recorded by other writers. Mr. Wardrop mentions ("Lancet," No. 516), that having removed a small tumour from behind the ear of a mother, all went well until she fell into a violent passion; and the child, being suckled soon afterwards, died in convulsions. He was sent for hastily to see another child in convulsions, after taking the breast of a nurse who had just been severely reprimanded; and he was informed by Sir Richard Croft that he had seen many similar instances. Three others are recorded by Burdach ("Physiologie," § 522); in one of them, the infant was seized with convulsions on the right side and hemiplegia on the left, on sucking immediately after its mother had met with some distressing occurrence. Another case was that of a puppy, which was seized with epileptic convulsions on sucking its mother after a fit of rage.

natural that no feeling should be stronger in the mother's mind under such circumstances, than the fear that her own beloved child should be taken from her, as that of her friend had been; and it is probable that she had been particularly dwelling on it, at the time of nursing the infant on that morning. —Another instance, in which the maternal influence was less certain, but in which it was not improbably the immediate cause of the fatal termination, occurred in a family nearly related to the Author's. The mother had lost several children in early infancy from a convulsive disorder; one infant, however, survived the usually fatal period; but whilst nursing him one morning, she had been strongly dwelling on the fear of losing him also, although he appeared a very healthy child. In a few minutes after the infant had been transferred into the arms of the nurse, and whilst she was urging her mistress to take a more cheerful view, directing her attention to his thriving appearance, he was seized with a convulsion-fit, and died almost instantly. Now although there was here unquestionably a predisposing cause, of which there is no evidence in the other cases, it can scarcely be doubted that the *exciting* cause of the fatal disorder is to be referred to the mother's anxiety. This case offers a valuable suggestion,—which, indeed, would be afforded by other considerations, that an infant under such circumstances should not be nursed by its mother, but by another woman of placid temperament, who has reared healthy children of her own.

683. There is abundant evidence that a *sudden* and *violent* excitement of some depressing Emotion, especially Terror, may produce a severe and even a fatal disturbance of the Organic functions; with general symptoms (as Guislain* has remarked) so strongly resembling those of sedative Poisoning, as to make it highly probable that the *blood* is *directly* affected by the Emotional state, through nervous agency; and in fact, the emotional alteration of various secretions, just alluded to (§§ 680–682), seems much more probably attributable to some affection of the blood, than to a primary disturbance of the secreting process itself. Although there can be no doubt that the *habitual* state of the Emotional sensibility has an important influence upon the general activity and perfection of the Nutritive processes—as is shown by the well-nourished appearance usually exhibited by those who are free from mental anxiety as well as from bodily ailment, contrasted with the "lean and hungry look" of those who are a prey to continual disquietude—yet it is not often that we have the opportunity of observing the production of change in the nutrition of any specific part, by strong emotional excitement. In the two following cases, the correspondence of the effects to their alleged causes *may* have been only casual; and a much larger collection of facts would be needed to *establish* the rationale here advanced as probable. But so many analogous though less strongly-marked phenomena are presented in the records of medical experience, and the influence of the Emotions upon the products of Secretion is so confirmatory, that there does not seem any reasonable ground for hesitation, in admitting that the same explanation may apply here also. The first of these cases, cited by Guislain (loc. cit.) from Ridard, is that of a woman who, after seeing her daughter violently beaten, was seized with great terror, and suddenly became affected with gangrenous erysipelas of the right breast. But a still more remarkable example of local disorder of nutrition, occasioned by powerful emotion, and determined as to its seat by the intense direction of the attention to a particular part of the body, is narrated by Mr. Carter.† "A lady who was watching her little child at play, saw a heavy window-sash fall

* "Leçons Orales sur les Phrénopathies," tom. iii. pp. 165–168.

† "On the Pathology and Treatment of Hysteria," p. 24.

upon its hand, cutting off three of the fingers; and she was so much overcome by fright and distress as to be unable to render it any assistance. A surgeon was speedily obtained, who, having dressed the wounds, turned himself to the mother, whom he found seated, moaning, and complaining of pain in her hand. On examination, three fingers, corresponding to those injured in the child, were discovered to be swollen and inflamed, although they had ailed nothing prior to the accident. In four-and-twenty hours incisions were made into them, and pus was evacuated; sloughs were afterwards discharged, and the wounds ultimately healed."

684. The influence of the state of *expectant attention*, in modifying the processes of Nutrition and Secretion, is not less remarkable than we have already seen it to be in the production or modification of Muscular movements (§ 676). It seems certain that the simple *direction of the consciousness* to a part, independently of emotional excitement, but with the *expectation* that some change will take place in its organic activity, is often sufficient to induce such an alteration; and would probably always do so, if the concentration of the attention were sufficient. The most satisfactory exemplification of this principle has been given by the experiments of Mr. Braid, who has succeeded in producing very decided changes in the secretions of particular organs, by the fixation of the attention upon them in the 'hypnotic' state* (§ 540). Thus he brought back an abundant flow of milk to the breast of a female who was leaving off nursing from defect of milk, and repeated the operation upon the other breast a few days subsequently, after which the supply was abundant for nine months; and in another instance he induced the catamenial flow on several successive occasions, when the usual time of its appearance had passed. It is not requisite, however, to produce the state of Somnambulism for this purpose, if the attention can be sufficiently drawn to the subject in any other mode; thus Mr. Braid† has repeatedly produced the last-named result on a female who possessed considerable power of mental concentration, by inducing her to fix her thoughts upon it for ten or fifteen minutes, so as to bring on a state of Abstraction.—Now the effects which are producible by this *voluntary* or determinate direction of the consciousness to the result, are doubtless no less producible by that *involuntary* fixation of the attention upon it, which is consequent upon the eager expectation of benefit from some curative method in which implicit confidence is placed. It is to such a state that we may fairly attribute most, if not all, the cures, which have been worked through what is popularly termed the 'imagination.' The cures are real facts, however they may be explained; and there is scarcely a malady in which amendment has not been produced, not merely in the estimation of the patient, but in the more trustworthy opinion of medical observers, by practices which can have had no other effect than to *direct the attention* of the sufferer to the part, and to keep alive his *confident expectation* of the cure. The 'charming-away' of warts by spells of the most vulgar kind, the imposition of royal hands for the cure of the 'evil,' the pawings and strokings of Valentine Greatrakes, the manipulations practised with the 'metallic tractors,'‡ the invocations of

* 'On the subject of Hypnotism,' see "Brit. Med. Journ." vol. ii., p. 381, 1880, and "The Nineteenth Century," Sept., 1880.

† See his important Memoir on 'Hypnotic Therapeutics,' in "Edinb. Monthly Journal," July, 1853.—Of the reality of this last result, the Author has had an opportunity, through Mr. Braid's kindness, of personally satisfying himself.

‡ Dr. Haygarth, of Bath (in conjunction with Mr. Richard Smith, of Bristol), tested the value of 'Perkin's metallic tractors' by substituting two pieces of wood painted in imitation of them, or even a pair of tenpenny nails disguised with sealing-wax, or a couple of slate-pencils; which they found to possess all the virtues that were claimed for the real instruments.

Prince Hohenlohe, *et hoc genus omne*—not omitting the globulistic administrations of the Infinitesimal doctors, and the manipulations of the Mesmerists, of our own times,—have all worked to the same end, and have all been alike successful. It is unquestionable that, in all such cases, the benefit derived is in direct proportion to the *faith* of the sufferer in the means employed; and thus we see that a couple of bread-pills will produce copious purgation, and a dose of *red* poppy syrup will serve as a powerful narcotic if the patient have entertained a sufficiently-confident expectation of such results.*

685. This state of confident expectation, however, may operate for evil, no less than for good. A fixed belief that a mortal disease had seized upon the frame, or that a particular operation or system of treatment would prove unsuccessful, has been in numerous instances (there is no reason to doubt) the direct cause of a fatal result. Thus M. Ridard relates the case of a man, thirty years of age, who was affected with stone in the bladder, and who saw a patient die by his side, after being operated upon for the same complaint. The man's imagination became excited; his thoughts were constantly fixed upon the operation which he himself expected to undergo, and upon the probable death that would follow; and in fact, without any operation at all, he died at the end of a month, affected with gangrene both of the penis and scrotum. Hence also, it is that the morbid feelings of the Hypochondriac, who is constantly directing his attention to his own fancied ailments, tend to induce real disorder in the action of the organs which are supposed to be affected.—In the same category, too, may be placed those instances (to which alone any value is to be attached), wherein a *strong and persistent impression* upon the mind of a Mother, has appeared to produce a corresponding effect upon the development of the *fœtus in utero*. In this case, the effect (if admitted to be really exerted) must be produced upon the maternal *blood*, and transmitted through it to the fœtus; since there is no nervous communication between the parent and the offspring. There is no difficulty, however, in understanding how this may occur, after what has been already stated (§ 203 *et seqq.*) of the influence of minute alterations in the Blood in determining local alterations of nutrition.

CHAPTER XVIII.

OF GENERATION.

1. *General Character of the Function.*

686. HAVING now passed in review the various operations which are concerned in maintaining the life of the *individual*, we have next to proceed to those whose are destined to the perpetuation of the *race* by the production of successive generations of similar beings. The question of the occurrence of spontaneous generation is one that has received great attention during the last few years, but the opinions that have been expressed both for and against it are still *sub judice*. No doubt can be entertained that under all ordinary circumstances fluids containing organic substances in solution or suspension when exposed to temperatures of 40° and 100° or 110° F., and more rapidly as the mean temperatures of 70° and 80° are approximated, exhibit evidences of life. The fluid—such, for instance, as an infusion of turnip, carrot, meat,

* A remarkable and thoroughly well-attested case of the cure of a fistula lachrymalis, which had advanced so far as to involve disease of the bones of the nose, is recorded in the "History of the Portroyalists."

cheese—becomes cloudy, from the formation or separation of an infinite number of minute molecules, almost unresolvable by the highest microscopic powers. Soon Bacteria, or small rod-shaped bodies appear, which exhibit movements of a slow oscillating character, then more swiftly-moving monads and vibrios, and, finally, infusoria of various forms and more complex structure. Two views have been advanced to explain the development of these lowly-organized beings. On the one hand, the *panspermists* maintain that the air is crowded with spores so small as to be imperceptible to the highest microscopic powers, and which, falling on suitable soil, as into moist solutions of organic substances, immediately begin to increase and multiply ; and they point to the fact that the purer the air, whether it be that obtained on high mountain-tops, or which has been filtered through cotton wool, or has been made to pass through red-hot tubes, the less likely is the solution, if protected by closing the mouth of the vessel in which it is contained, to become the seat and focus of life. On the other hand, the *heterogenists* contend that, as on the Darwinian theory pushed to its furthest limit, the whole animal and vegetable kingdoms may be derived from some simple form, which must have originated from the action of light and heat, or of heat alone, on the inorganic materials of which the earth is composed, it is not unlikely that the same process is constantly being repeated when the appropriate conditions are present ; and they point as additional arguments in favour of their view, to the circumstances that, whatever may be the care taken in filtering the air admitted to organic infusion, and even when a boiling temperature has been maintained for several minutes with hermetic closure of the vessel during the process of ebullition, it is, in many cases, impossible to prevent the development of Bacteria, though the absence or great diminution of air, or rather of oxygen, thus occasioned prevents them forming in any considerable numbers. They refer also to the extraordinary numbers in which the Bacteria appear—numbers which they believe to be incompatible with their production from the spores supposed by the panspermists to be floating in the air ; and, lastly, they refer to various experiments which seem to show that the lowest forms of life may be germinated in solutions consisting exclusively of inorganic compounds. When it is considered how difficult it is to preserve the air admitted to the solution used in these experiments in a perfect state of purity, and our ignorance of the amount of heat which the spores of the lower organisms can bear exposure to without destruction, it would seem at present that it is safest to hold the doctrine of panspermism, though it must be admitted to present several points of considerable difficulty.*

687. Among Plants, and the lower tribes of Animals, a multiplication of independent beings takes place without any sexual process whatever, by a process of *gemmation* or 'budding' from the parent-stock ; these 'buds,' at first entirely nourished by it, gradually become less and less dependent upon it, and at last detach themselves and maintain a separate existence. Now this process may be regarded as essentially the same with that of the multiplication of cells by *subdivision*, which is one of the most ordinary operations of growth and development; and it is peculiar in nothing else than this,—that the newly-formed structure, instead of remaining as a constituent and dependent part of the parental fabric, is capable of living independently of it, and of thus existing as a distinct individual when spontaneously or artificially detached. Among the higher tribes of Animals, as in Man, this mode of

* The student will find a very full discussion, with an historical résumé of this subject, in Dr. Bastian's "Beginnings of Life," 1872 ; Burdon Sanderson, "Nature," vol. viii. p. 478 ; Heuzinger, Samuelson, Putzeys, and Gscheidlen, in Pflüger's "Archiv," for 1873 and 1874.

reproduction, which is merely a multiplication of the individual, and not a real Generative process, does not present itself, at least in the adult state; for in no instance do we find that a part of the body separated from the rest can develop the organs which are necessary for the sustenance of its existence; and the power which the organism possesses, of regenerating parts which it has lost by disease or accident, is restrained within very narrow limits (§ 333). But there is good ground to believe, that such a multiplication by subdivision *may* take place at that earliest period of embryonic life, at which the germ is nothing else than a mass of cells, wherein no distinction of parts has as yet manifested itself; and that the production of two complete individuals, held together only by a connecting band, may arise from some cause which determines the subdivision of the germinal mass, at the period when its grade of development corresponds with that of the Hydra or Planaria. And this view of the case is confirmed by the facts already stated (§ 333) in regard to the higher degree of the regenerating power during embryonic life, infancy, and childhood, as compared with that which remains after the development of the fabric has been completed.

688. The proper act of Generation in Man, as in the Animal and Vegetable Kingdoms generally (see PRINC. OF COMP. PHYS., Chap. XI.), uniformly involves the union of the contents of two peculiar cells, which may be designated as the 'sperm-cell' and the 'germ-cell.' In all the higher Animals, the 'sperm-cell' develops a self-moving *spermatozoon*, whilst the 'germ-cell' (germinal vesicle), whose contents are fertilized by the spermatozoon, is embedded in a mass of *yolk* destined for the early nutrition of the embryo thence originating: so that this embryo, when supplied with the requisite warmth, as well as drawing into itself the aliment stored-up for it, gradually evolves itself into the likeness of its parent. There is a great difference, however, among the different tribes of Animals, as to the degree of assistance thus afforded to the embryo,* the general rule being, that the higher the form which the embryo is ultimately to attain, the longer is it supported by its parent. Hence we find the embryos of most Invertebrate animals coming-forth from the egg in a condition very unlike their perfect type, and only acquiring this after a long succession of subsequent alterations, which frequently involve a complete change of form, or *metamorphosis*. In Fishes, however, the embryo, though far from having completed its embryonic development at the time of its emergence from the egg, does not differ so widely from the adult type. In Birds, there is a provision for a much more advanced development; the store of nutritious matter, or 'yolk,' being so large as to allow the whole series of changes requisite for the formation of the complete chick to take place before it leaves the egg. In the Mammalia, on the contrary, the quantity of yolk contained in the ovum is very small, but the embryo is only dependent upon it for the materials of its increase during the earliest stages of its evolution; for it speedily forms a special connection with the parent structure, by means of which it is enabled to receive a continual supply of newly-prepared aliment, so as to be supported at the expense of this until far advanced in its development. Some approaches to this arrangement are met with among certain of the lower animals, but it is only in the higher Mammalia that it is completely carried out; and it is only in this class, too, that we find a supplemental provision for the nutrition of the offspring after it has come forth into the world.† In many of the lower tribes of animals,

* For an account of these varieties, see "The Life Histories of Animals, including Man," by A. S. Packard, New York, 1876; and "Comparative Embryology," by F. M. Balfour, F.R.S. Macmillan, 1880.

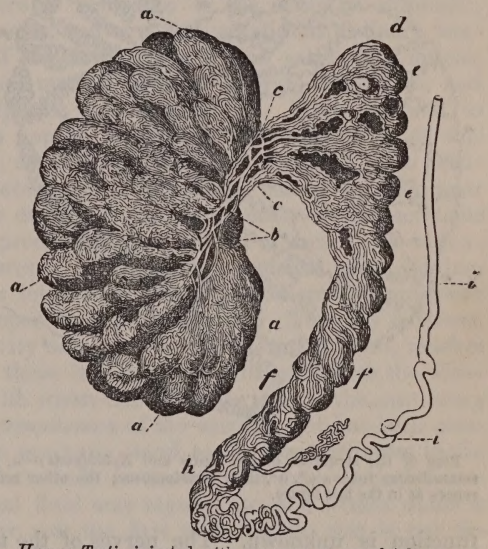
† For different types of segmentation, *vide infrd.*

the fertilization of the ova is accomplished without any sexual congress; the spermatic fluid effused by the male coming into direct contact with the ova previously deposited by the female; but in all the higher tribes, as in Man, the spermatic fluid is conveyed into the oviducts of the female, so as to impregnate the ovum shortly after it has quitted the ovarium, or even before its final escape from it.

2. *Action of the Male.*

689. The Spermatic fluid of the Male is secreted by glandular organs known as *Testes*. Each of these consists of several lobules, which are separated from each other by processes of the Tunica Albuginea that pass down between them, and also by an extremely delicate membrane (described by Sir A. Cooper under the name of Tunica Vasculosa) consisting of minute ramifications of the spermatic blood-vessels united by areolar tissue. Each lobule (Fig. 308, *a a*) is composed of a mass of convoluted *tubuli seminiferi*, throughout which blood-vessels are minutely distributed. The lobules differ greatly in size, some containing one, and others many of the tubuli; the total number of the lobules is estimated at about 450 in each testis, and that of the tubuli at 840. The walls of the tubuli are firmer than those of similar gland-canals elsewhere; for the basement-membrane on which the epithelium rests, consists of a tolerably firm but extensible envelope, composed of a hyaline elastic membrane with oval flattened nuclei. They are lined by several layers of epithelial cells—the seminal cells.* These cells may be divided into outer cells, situated next to the membrana propria, and inner cells, nearer to the lumen. The inner cells are generally arranged in more than two layers; they are polyhedral, possess a transparent spherical nucleus, and are separated from each other by a clear interstitial matrix, the *germ reticulum*. The cells present evidences of undergoing rapid multiplication, and exhibit amœboid movements. The convolutions of the tubuli are so arranged that each lobule forms a sort of cone, the apex of which is directed towards the *rete testis* (*b*); and when they have reached to within a line or two of this, they cease to be convoluted, and several unite together into tubes of larger diameter, which enter the rete testis under the name *tubuli recti*. The mode in which the tubuli terminate at the large end of the lobule has not been clearly made-out, owing partly to the number of their

FIG. 308.

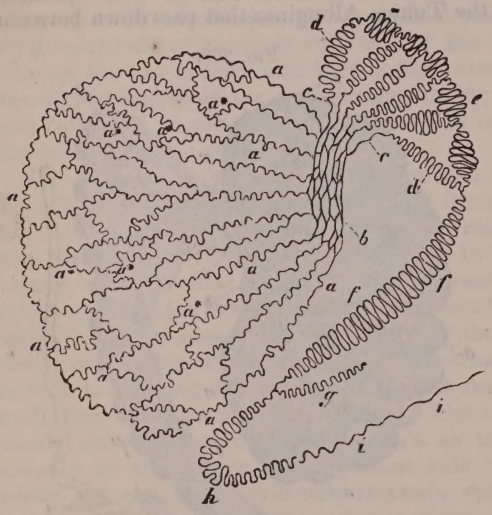


Human Testis, injected with mercury as completely as possible: *a*, *a*, lobules formed of seminiferous tubes; *b*, rete testis; *c*, vasa efferentia; *d*, flexures of the efferent vessels passing into the head, *e*, *e*, of the epididymis; *f*, body of the epididymis; *g*, appendix; *h*, cauda; *i*, vas deferens.

* V. Lavalette St. George, Stricker's "Handbook of Histology," Syd. Soc. Trans., 1872, vol. ii. p. 139; and Klein and Noble's "Atlas of Histology," pp. 270-272.

anastomoses; it is probably either by cæcal endings or by loops. The diameter of the tubuli is for the most part very uniform; in the natural condition they seem to vary from about the 1-195th to the 1–70th of an inch; but when injected with mercury, they are distended to a size nearly double the smaller of these dimensions.—The *rete testis* (*b*) consists of from seven to thirteen vessels, which run in a waving course, anastomose with each other, and again divide, being all connected together. Each tubulus, and each vessel of the rete testis, consists of a hyaline membrana propria lined with a single layer of short transparent columnar cells. The *vasa efferentia* (*c*), which pass to the head of the epididymis, are at first straight, but soon become convoluted (*d*), each forming a sort of cone, of which the apex is directed towards the rete testis, the base to the head of the epididymis (*e*). The number of these is stated to vary from nine to thirty; and their length to be about eight inches. The *epididymis* (*f*) consists of a very convoluted canal, the length of which is about twenty-one feet. Into its lower extremity, that is, the angle which it makes where it terminates in the vas deferens, is attached an appendix (*g*) composed of one or more *vasa aberrantia;* which, like the epididymis, are lined with columnar ciliated epithelium. Their special function is unknown. The nerves of the testis are stated by Letzerich* to pierce the membrana propria of the tubuli seminiferi, and end in a more or less irregular pyramidal mass of protoplasm, in which lie clear elliptic nuclei. The ends of the fibres, therefore, lie in close relation to the outer layer of secreting cells. The lymphatic channels in the testis are numerous, and in the epididymis extend as a delicate meshwork of vessels as far as the vas deferens.

Fig. 309.



Plan of the structure of the *Testis* and *Epididymis*:—*a*, *a*, seminiferous tubes; *a**, *a**, their anastomoses; the other references as in the last figure.

690. The fluid secreted by the Testis is invariably alkaline in Man, and is mingled, during or previously to its emission, with fluid secreted by the Vesiculæ Seminales, the Prostate, Cowper's glands, &c.; and it cannot, therefore, be obtained pure, except by drawing it from the testicle itself. No accurate analysis of it has been made in the human subject; but Kölliker† has made the following analysis of it in the Bull and Stallion:—

	Bull.	Stallion.
Water	820·60	819·40
Solid residue	179·40	180·60
Spermatin and Extractives	153·0	164·49
Fat	21·6	—
Salts	26·37	16·11

* Virchow's "Archiv," March, 1868.

† v. Gorup-Besanez, 1862, "Phys. Chem.," p. 424.

Frerichs,* on examining the contents of the Testes of a Rabbit, a Cock, and a Carp, found pure Semen to be a milky fluid of a mucous consistence, and neutral or slightly-alkaline reaction. That of the Bull is acid (Miescher). The principal organic substances of the mature semen in the Salmon are thus given by Miescher†:—Nuclein, 48·68 per cent.; Protamin ($C_9H_{20}N_5O_2$), 26·76; Albuminous Compounds, 10·32; Lecithin, 7·47; Cholesterin, 2·24; Fat, 4·53. The spermatozoa of the Bull contain no Protamin, but consist of Nuclein (50 per cent.), Albumin, and a body containing much phosphorus. Protamin is a non-crystallized substance of glutinous consistence, soluble in water, to which it gives an alkaline reaction, and is insoluble in alcohol and ether. It combines both with metallic bases and with acids. A substance named Spermatin, resembling alkali albumin, and mucin, has also been obtained from Semen. The ashes contain 5 per cent. of phosphate of lime. The spermatozoa evince little tendency to decomposition, and offer considerable resistance to the action of sulphuric, nitric, hydrochloric, and acetic acids, and to caustic alkalies at ordinary temperatures. The fluid portion of the secretion is a thin solution of mucus, which, in addition to the animal matter, contains chloride of sodium, and small quantities of alkaline sulphates and phosphates. When allowed to evaporate spontaneously, crystals appear, which are composed either of ammonio-magnesium phosphate, or, as Böttcher thinks, of albumin. The peculiar odour which the Semen possesses does not appear to belong to the proper spermatic fluid; but is probably derived from one or other of the secretions with which it is mingled.—The product of the secretion of each Testis is conveyed away by a single *vas deferens* (*i*), which is a cylindrical canal, having, within its fibrous wall, a circular longitudinal layer of non-striated muscular fibre, and being lined by a proper mucous membrane. The vas deferens, ascending into the abdominal cavity as a part of the spermatic cord, reaches the fundus of the bladder; and there it comes into proximity with the *Vesicula Seminalis* of its own side, with whose duct it unites to form the *ejaculatory duct* which terminates on the *verumontanum* of the urethra. It has been commonly supposed that the *vesiculæ seminales* stand to the *vasa deferentia* in the same light that the gall-bladder stands to the hepatic duct—namely, as a receptacle into which the seminal fluid may regurgitate, and within which it may accumulate; but (as Hunter was the first to maintain) this is not the case, since the fluid that is found in them is not semen, and but rarely contains even a small admixture of seminal fluid.‡ Moreover, these organs are not simple vesicles, but have a sacculated glandular character; and their secretion seems to be of a mucous nature. Into the same part of the urethra is discharged the secretion of the *Prostate Gland*, which is poured forth by a number (15–20) of separate ducts into a depressed fossa on either side; of the nature of this secretion scarcely anything is known; it contains 98·5 per cent. of water, and it may be surmised that its use, like that of the fluid of the vesiculæ seminales, is to dilute the seminal fluid, and to give it such an increase of bulk that it may be more effectually conveyed within the female passages. It seems probable, indeed, that a certain dilution of the fluid secreted by the testes may be a condition of its power of fecundation; since it has been ascertained by Mr. Newport, that too copious an application of spermatozoa to an ovum is absolutely unfavourable to their action.—That in some way or other both these glandular bodies serve as accessory organs of generation, may be inferred from the fact, that in animals which have only a periodical aptitude for pro-

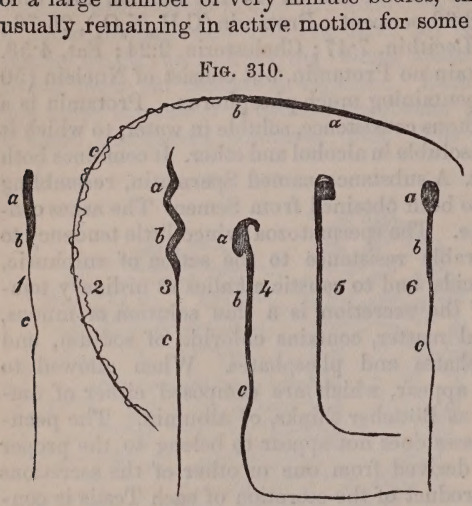
* Art. 'Semen,' in "Cyclop. of Anat. and Physiol.," vol. iv. p. 506.

† Quoted in v. Gorup-Besanez, "Physiolog. Chemie," 1874, p. 463.

‡ See Art. 'Vesiculæ Seminales,' in "Cyclop. of Anat. and Physiol.," vol. iv. p. 1431.

creation, they undergo an alternate increase and decrease, corresponding with the periodical enlargement and diminution of the testes themselves. The essential peculiarity of the Spermatic fluid, however, consists in the presence of a large number of very minute bodies, the *spermatozoa*, which, from their usually remaining in active motion for some time after they have quitted the living organism, have been erroneously considered as proper Animalcules. The Human Spermatozoon (of which representations are given in Plate I., Fig. 1; whilst some of the principal forms in other animals are shown in Fig. 310) consists of a small oval flattened discoid 'head,' 5 μ* in length and 1–2 μ in thickness, an intermediate portion 6 μ in length, from which proceeds a long filiform 'tail' gradually tapering to the finest point, of 50 μ in length. The whole is perfectly transparent; and nothing that can be termed 'structure' can be satisfactorily distinguished within it.† Its movements are principally executed by the tail, which has a kind of vibratile undulating motion, by means of which the head is driven forwards. The rate of progression of spermatozoa has been stated to be ·004 mm. per second; and they move with sufficient force to displace calcareous particles ten times their own bulk. Their movements may continue for many hours after the emission of the fluid; and they are not checked by its admixture with other secretions, such as the urine and the prostatic fluid. Thus, in cases of nocturnal emission, the spermatozoa may not unfrequently be found actively moving through the urine in the morning; and those contained in the seminal fluid collected from females that have just copulated, are frequently found to live many days. As in the case of ciliated epithelium, the movements are rapidly arrested by weak acids, whilst they are stimulated by alkalies. They cease when the

FIG. 310.



1. Spermatozoon of the frog.
2. „ „ triton.
3. „ „ finch.
4. Spermatozoon of the field-mouse.
5. „ hedgehog.
6. „ sheep.

a. Head with nucleus. *b*. Body. *c*. Tail.

* μ = ·001 of a millimètre.

† The characteristic forms of the spermatozoa of the various classes of the Vertebrata, are beautifully represented by Schweigger-Seidel in Max Schultze's "Mikroskop. Anat.," Band i. p. 309. He describes each spermatozoon as consisting of a head, body, and tail, the latter, as in some tritons, having a membrane attached to it, which performs undulatory movements. Grohe (Virchow's "Archiv," Band xxxii. p. 401) attributes the movements of the spermatozoa to the contractile protoplasm contained in the 'head' of the zooid; Bizzozero to that in the cilium or tail. See also v. Lavalette St. George, Art. 'Testes,' in Stricker's "Hum. and Comp. Histology," Syd. Soc. Transl., 1872, vol. ii. p. 149; Heneage Gibbes ('On the Structure of the Vertebrate Spermatozoon,' "Quarterly Journal of Microscopical Science," vol. xix. p. 487) distinguishes two distinct substances in the Spermatozoon, one in the head, the second forming the filament. This author also shows that the spermatozoon in the salamander and triton, and probably also in Mammalia consists of (*a*) a long head; (*b*) an elliptical portion connecting it with (*c*) the filiform body; (*d*) a very fine long thread, which is united to the body by (*e*) a homogeneous membrane. The motive power lies in a great measure in the filament, and the membrane attaching it to the body. The head of the spermatozoon is enclosed in a sheath which is the continuation of the membrane which surrounds the filament, and connects it to the body.

spermatozoa are exposed to a temperature of 120° F.,* but frozen spermatozoa recommence movements on being thawed.

691. The mode of evolution of the Spermatozoa,† which are undoubtedly true products of the formative action of the organs in which they are found, and cannot be ranked in the same category with the Protozoa, probably varies in different animals, so that in one the entire sperm-cell with all its parts is converted into a Spermatozoon (Schweigger-Seidel); in another the Spermatozoon proceeds exclusively from the nucleus (Kölliker), and in another it originates from the nucleus which remains as the head, and the cell-protoplasm which develops into the tail (v. Lavalette St. George).‡ This latter theory has been adopted by Klein,§ who states that certain cells lying nearest to the lumen of the seminal tubes, and named *spermatoblasts*, undergo changes which result in the nuclei becoming excentric, flattened, and oblong, forming the head, which is probably invested by a covering of the cell substance. The tail of the spermatozoon is formed by the rest of the cell contents, which is at first club-shaped, but is afterwards modified into a long, thin, and homogenous filament. M. Duval,‖ on the other hand, states that at puberty, amongst the epithelial cells lining the tubuli seminiferi, large cells may be distinguished, which he names 'mother cells,' and which result from the development of the primitive globules. These cells are comparable with the ovule of the female. Ch. Robin names them 'male ovules.' In different animals these cells proliferate either by endogenous multiplication or by gemmation, and give rise to a group of young cells named spermatoblasts, each of which becomes a spermatozoon. This change is completed, and the spermatozoa become free in the epididymis. The protoplasm of the spermatoblast forms the nuclear enlargement of the head of the spermatozoon and the tail, but it is doubtful whether the nucleus is preserved in the head. Besides the cells already described, numerous molecules are found in the semen. Mr. Gulliver describes them as resembling oil-particles, and varying in diameter from 1–20,000th to 1–8000th of an inch. They are always present, but are particularly abundant in birds and reptiles, when the testes begin to enlarge in spring, and become scanty as soon as the spermatozoa are completely developed. And the same is true for Man just before and after the attainment of the age of puberty.

692. That the Spermatozoa are the essential elements of the spermatic fluid, may be reasonably inferred from several considerations. There are some cases in which the 'liquor seminis' is altogether absent, so that they constitute the sole element of the semen; whilst, on the other hand, they are never wanting in the semen of animals capable of procreation; but are absent or imperfectly developed in the semen of hybrids, which are nearly or entirely sterile. Moreover, it may be considered as certain that the absolute contact

* See Bizzozero, "Annali Universali," vol. clxxxvii.

† For researches on the development, &c. of the Spermatozoa, see the elaborate Article 'Semen,' in the "Cyclop. of Anat. and Physiol.," by Drs. Wagner and Leuckart; Prof. Kölliker's "Manual of Microscopic Anatomy," 1860; Schweigger-Seidel in Max Schultze's "Archiv f. Mikroskop. Anat.," Band i. p. 309; v. Lavalette St. George, Stricker's "Human and Comp. Histology," vol. ii. 1872, p. 131; Merkel, "Reichert's Archiv," 1871, p. 644; Neumann ("Centralblatt," 1872, p. 881) contends that Spermatozoa are merely detached cilia developed from the epithelial cells lining the tubuli testis. See also v. Ebner, Reichert's "Archiv," 1872, p. 250; Henle, "Handbuch," Band ii. p. 356. G. Balbiani, "Leçons sur la génération des Vertébrés," Paris, 1879; J. E. Blomfield, "Quarterly Journ. Micros. Sci.," vol. xx. p. 80.

‡ Kölliker's views on the development of the spermatozoa are illustrated in Plate I., Figs. 2 and 3.

§ "Atlas of Histology," pp. 272–276.

‖ "Récherches sur la Spermatogenèse," Paris, 1878.

of the spermatozoa with the ovum is requisite for its fecundation; whilst, on the other hand, if the spermatozoa be carefully removed from the liquor seminis by filtration, the latter is entirely destitute of fertilizing power.* Hence the presence of the Liquor Seminis must be considered as merely incidental; and as answering some secondary purpose, either in the development or in the conveyance of the Spermatozoa. Henle† observes that whilst the Spermatozoa retain their vitality even in extreme old age, they are frequently absent in the seminal fluid of those suffering from disease.‡

693. The power of procreation does not usually exist in the Human Male before the age of from 14 to 16 years; and it may be considered probable that no Spermatozoa are produced until that period, although a fluid is secreted by the testes. At this epoch, which is ordinarily designated as that of *Puberty*, a considerable change takes place in the bodily constitution; the sexual organs undergo a much increased development; various parts of the surface, especially the chin and the pubis, become covered with hair; the larynx enlarges, and the voice becomes lower in pitch, as well as rougher and more powerful; and new feelings and desires are awakened in the mind. Instances, however, are by no means rare, in which these changes occur at a much earlier period; the full development of the generative organs, with manifestations of the sexual passion, having been observed in children but a few years old. The procreative power may last, if not abused, during a very prolonged period. Undoubted instances of virility at the age of more than 100 years are on record; but in these cases the general bodily vigour was preserved in a very remarkable degree. The ordinary rule seems to be, that sexual power is not retained by the male, to any considerable amount, after the age of 60 or 65 years.

694. To the use of the sexual organs for the continuance of his race, Man is prompted by a powerful instinctive desire (§ 510), which he shares with the lower animals. This Instinct, like the other propensities, is excited by sensations; and these may either originate in the sexual organs themselves, or may be excited through the organs of special sense. Thus in Man it is most powerfully aroused by impressions conveyed through the sight or the touch; but in many other animals, the auditory and olfactory organs communicate impressions which have an equal power; and it is not improbable that, in certain morbidly-excited states of feeling, the same may be the case in ourselves. Localized sensations have also a very powerful effect in exciting sexual desire, as must have been within the experience of almost every one; the fact is most remarkable, however, in cases of Satyriasis, which disease is generally found to be connected with some obvious cause of irritation of the generative system, such as pruritus, active congestion, &c. That some part of the Encephalon is the seat of this as of other instinctive propensities appears from

* This point was completely established by the researches of Mr. Newport ("Phil. Trans.," 1851), who repeated and confirmed the experimental results previously obtained by Spallanzani and by Prévost and Dumas.

† "Anatomie des Menschen," p. 357.

‡ This observation has been supported by Mantegazza and Bozzi, who found that in 88 cases of various forms of disease, on examination of the Testis the spermatozoa were deficient in both organs in 12 cases, and in one testis in 9 cases, whilst this could only be referred to organic lesion of the testis in two cases. Gulliver 'On the Semen and Seminal Tubes of Mammals and Birds' ("Proc. Zool. Soc.," July, 1842; and "Edin. Med. and Surg. Journ.," 1843, vol. lx. p. 158), also gives many examples of the absence of spermatozoa in cases of disease in Man and the lower Animals, and in birds during the winter. He has found that the spermatozoa of a particular genus may differ remarkably in chemical and other characters. Thus in the Fringillidæ they are quickly dissolved by acetic acid and other reagents, which have no action on the club-shaped spermatozoa of Hirundinidæ.

the considerations formerly adduced; but that the Cerebellum is the part in which this function is specially located cannot be regarded as by any means sufficiently proved (§§ 507–510). The instinct, when once aroused (even though very obscurely felt), acts upon the mental faculties and moral feelings; and thus becomes the source, though almost unconsciously so to the individual, of the tendency to form that kind of attachment towards one of the opposite sex which is known as *love*. This tendency cannot be regarded as a simple passion or emotion, since it is the result of the combined operations of the reason, the imagination, and the moral feelings; and it is in this engraftment (so to speak) of the physical attachment, upon the mere corporeal instinct, that a difference exists between the sexual relations of Man and those of the lower animals.

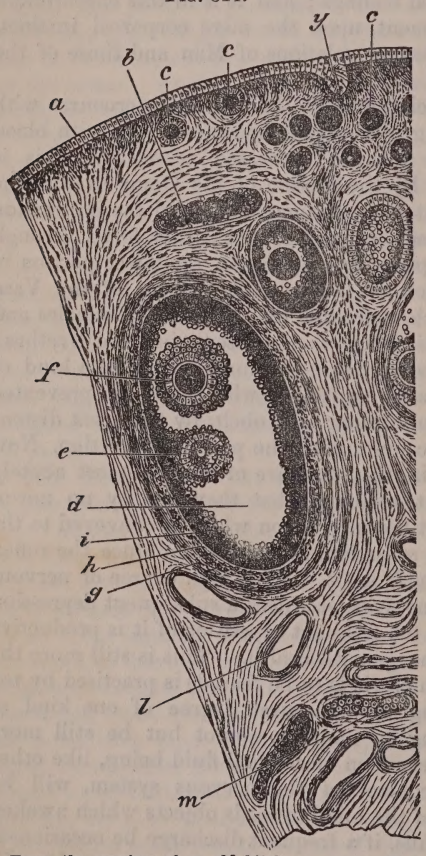
695. When, impelled by sexual excitement, the Male seeks intercourse with the Female, the erectile tissue of the genital organs becomes turgid with blood (§ 257), and the surface acquires a much increased sensibility; this is especially acute in the Glans penis. By the friction of the Glans against the rugous walls of the Vagina the excitement is increased; and the impression which is thus produced at last becomes so strong, that it calls forth, through the medium of a ganglionic centre, probably situated in the lower portion of the Spinal Cord, a reflex contraction of the muscular fibres of the Vasa Deferentia, and of the muscles which surround the Vesiculæ Seminales and Prostate gland. These receptacles discharge their contents into the Urethra; from which they are expelled with some degree of force, and with a kind of convulsive action, by its own Compressor muscles; whilst they are prevented from passing back into the bladder, according to Kobelt, by the great distension of the Verumontanum, which occurs during the period of erection. Now although the sensations concerned in this act are ordinarily most acutely pleasurable, there appears sufficient evidence that they are by no means essential to its performance; and that the impression which is conveyed to the Spinal Cord *need not* give rise to a sensation, in order to produce the reflex contraction of the Ejaculator muscles (§ 460). The high degree of nervous excitement which the act of coition involves, produces a subsequent depression to a corresponding amount; and the too frequent repetition of it is productive of consequences very injurious to the general health. This is still more the case with the solitary indulgence, which (it is to be feared) is practised by too many youths; for this, substituting an unnatural degree of one kind of excitement for that which is wanting in another, cannot but be still more trying to the bodily powers. The secretion of seminal fluid being, like other secretions, very much under the control of the nervous system, will be increased by the continual direction of the mind towards objects which awaken the sexual propensity (§ 680); and thus, if a frequent discharge be occasioned, whether by natural or unnatural excitement, a much larger quantity will altogether be produced, although the amount emitted at each period will be less, and its due perfection will not be attained, the fluid under such circumstances being found to contain an unduly-large proportion of immature seminal cells. The formation of the secretion seems of itself to be a much greater tax upon the corporeal powers than might have been supposed *à priori*; and it is a well-known fact, that the highest degree of bodily vigour is inconsistent with more than a very moderate indulgence in sexual intercourse; whilst nothing is more certain to reduce the powers, both of body and mind, than excess in this respect.—These principles, which are of great importance in the regulation of the health, are but expressions of the general law (which prevails equally in the Vegetable and in the Animal kingdom), that the Development

of the Individual and the Reproduction of the Species stand in an inverse ratio to each other, as has been well shown by Herbert Spencer.*

3. *Action of the Female.*

696. The essential part of the Female Generative system is that in which the Ova are prepared; the other organs are merely accessory, and are not to be found in a large proportion of the Animal kingdom. In many of the lower animals, the Ovarium consists of a loose tissue containing many areolæ, in which the Ova are formed, and from which they escape by the rupture of the cell walls; in the higher animals, as in the Human female, the substance of the Ovarium is firm and compact, and consists of a nucleated, tough, fibrous, connective tissue, with much interspersed fusiform muscular tissue forming what is known as the *stroma*. It originates in a small outgrowth of the inner surface of the Wolffian body, the regular columnar epithelial investment of which, probably derived from the epiblast, and contrasting strongly with the flattened epithelium of the rest of the peritoneal cavity, is thickened at this spot. The epithelium is the rudiment of the Graafian follicles and ova, whilst the out-growth is destined to form the vascular stroma of the ovary. As development proceeds the cells of the superficial columnar, or so-called germ epithelium multiply, and single cells or groups of cells, round, ovoid, or tubular, come to be enclosed in the tissue of the ovary by delicate vascular processes which shoot forth from the stroma. These cells constitute the primordial ova,† each of which is therefore a persistent cell of a peculiar epithelial formation. When mature a primordial ovum has a diameter of 200 μ (and

Fig. 311.



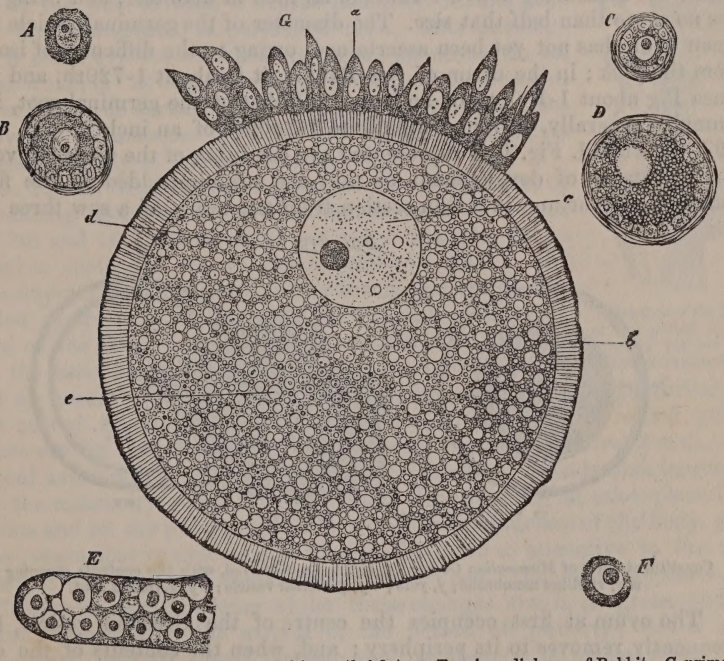
From the ovarium of an old bitch. *a*, germ epithelium; *b*, ovarian tube; *c c*, young Graafian follicles; *d*, older follicle; *e*, discus proligerus, with ovum; *f*, epithelium of a second ovum in the same follicle; *g*, fibrous tunic; *h*, tunica propria folliculi; *i*, epithelium of the follicle (membrana granulosa).

* "Principles of Biology," vol. ii. part vi. pp. 419–440.

† For the literature of the Histology of the Ovaries up to 1871, see Art. 'Ovary and Paro-varium,' by W. Waldeyer, in Stricker's "Hum. and Comp. Histology," Syd. Soc. transl., 1872, vol. ii. p. 164. Since then there have appeared Kapff, Reichert's "Archiv," 1872, p. 513, Foulis, "Trans. Royal Soc., Edinburgh," vol. xxvii. and Sernoff, "Centralblatt f. die Med. Wiss.," 1874, p. 481, denying, and Romiti, Schultze's "Archiv," Band x. p. 201, Born, Reichert's "Archiv," 1874, p. 118, and to a certain extent Balfour, "Quart. Journ. Micros. Sci.," vol. xviii. (1878), p. 383, and Klein, "Atlas of Histology," p. 291, corroborating Waldeyer's histological observations.

since μ represents a micromillimètre or 0·0000032809 of an inch, 200 μ would equal ·00065618, or about 1–524th of an inch), and is contained within a capsule termed the Graafian follicle or ovisac.* In a large Graafian follicle we may distinguish a connective tissue investing membrane, which is composed of two layers, the *tunica fibrosa* (*g*, Fig. 311), and the *tunica propria folliculi* (*h*); the latter is lined on its internal surface by several layers of cells, of which the nearest to the tunica propria are columnar, whilst the deeper ones are transparent and polyhedral (*i*), constituting the epithelium of the follicle, or *membrana granulosa*. The membrana granulosa is collected round each ovum into a disk-like investment termed the *discus proligerus* (*e*, Fig. 311), and the remainder of the follicular cavity contains a clear fluid, the *liquor folliculi*. The earliest rudiment of every ovum consists of a simple cell with soft granular protoplasm unenclosed by a

FIG. 312.



A, primordial egg of Man, from an eight months' fœtus; *B*, primordial egg of Rabbit; *C*, primordial follicle of a Pigeon; *D*, a somewhat older follicle from a Pigeon, showing commencing formation of secondary yolk; *E*, blind end of the ovary of an *Ascaris nigro-venosa*, showing germinal vesicle, germinal spot, and, in some instances, a Schrön's granule in a diffuse mass of protoplasm; *F*, egg of *Ascaris nig.* from about the middle of the ovary.

G, an Ovum from the Graafian Follicle of a Rabbit. *a*, epithelium of the ovum, part of the discus proligerus; *b*, radially striated zona pellucida; *c*, germinal vesicle; *d*, germinal spot; *e*, yolk.

membrane, a nucleus and a nucleolus. The protoplasm of the primordial cell is termed the formative or principal yolk, since it alone undergoes segmentation and development. The nucleus is termed the germinal vesicle (*Vesicula germinativa*) (*c*, Fig. 312; *v g*, Fig. 313), and the nucleolus, the germinal spot (*Macula germinativa*) (*d*, Fig. 312; *t g*, Fig. 313). According to Van Beneden,† the germinal vesicle in the ovum of the rabbit, and probably also of other mammalia, includes a clear liquid which is traversed by a granular substance,

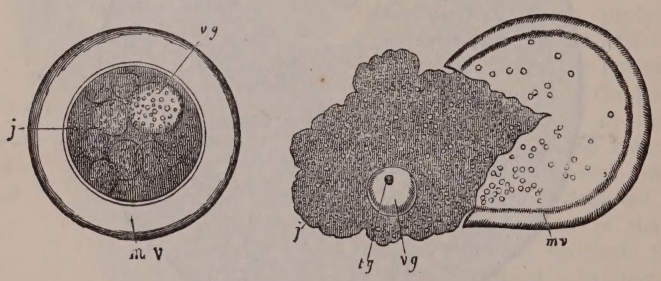
* Barry, 'Researches in Embryology,' 1st series, in "Philos. Transact.," 1838.

† "La Maturation de l'Œuf, la Fécondation et les premières Phases du Développement Embryonaire des Mammifères, d'après des récherches faites chez le Lapin," Bruxelles, 1875.

the nucleoplasm, which often forms a reticulum. Whilst still within the Graafian follicle the ovum becomes surrounded by a series of secondary formations, which are collectively to be regarded as products of the follicular epithelium. To these belong the vitelline membrane, or membrane enclosing the yolk, which on account of its thickness and peculiar transparency has received in Mammalia the distinctive appellation of *Zona pellucida** (*b*, Fig. 312; *m v*, Fig. 313), and the food yolk or secondary yolk. The zona pellucida in Mammals appears to be perforated by numerous fine pores, which confer upon it a striated aspect; through these pores it is supposed that the substance of the epithelial cells immediately surrounding the zona pellucida is continued in the form of fine threads; it is highly elastic, and when torn with needles the edges roll back and the contents issue in a stream. It resists to a considerable degree the action of acids and alkalies. When mature the Human Ovum is extremely minute; not measuring above 1-120th of an inch in diameter, and being sometimes no more than half that size. The diameter of the germinal vesicle of the Human ovum has not yet been ascertained, owing to the difficulty of isolating it from the yolk; in the ovum of the Rabbit, it is about 1-720th, and in the Guinea Pig about 1-1800th of an inch; and that of the germinal spot, in the Mammalia generally, is from 1-3600th to 1-2400th of an inch.

697. In Plate I. Fig. 4, is represented the condition of the Graafian vesicles in various stages of development, as they are seen imbedded in the fibrous stroma of the ovarium, in a thin section from the ovary of a sow three weeks

FIG. 313.



Constituent parts of *Mammalian Ovum*: A, entire; B, ruptured, with the contents escaping; *m v*, vitelline membrane; *j*, yolk; *v g*, germinal vesicle; *t g*, germinal spot.

old. The ovum at first occupies the centre of the Graafian vesicle, but it subsequently removes to its periphery; and, when the contents of the ovisac are undergoing maturation, prior to their escape, the ovum is always found on the side of it nearest to the surface of the ovary. The proper Ovisac, whose wall is formed of a non-vascular membrane, is surrounded by a vascular layer, which is formed by a condensation of the ordinary stroma of the ovarium; it is this which is usually described as the outer layer of the Graafian vesicle.

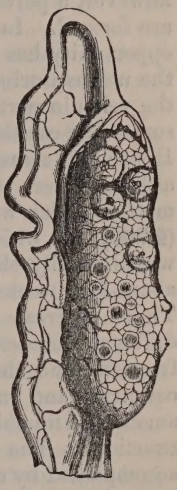
698. A continual change seems to be taking place in the contents of the Ovarium during the greater part of life; certain of the Ovisacs or Graafian vesicles, and their contents, successively arriving at maturity, whilst others degenerate and die. According to the valuable inquiries of Dr. Ritchie,† it appears that even during the period of childhood, there is a continual rupture

* Foulis (loc. cit., p. 378), in opposition to other observers, states that the vitelline membrane is formed by a hardening of the outer part of the yolk.

† "London Medical Gazette," 1844. See also Foulis, "Brit. Med Journ.," 1875, p. 841.

of ovisacs and discharge of ova, at the surface of the ovarium. The Ovaria are studded with numerous minute copper-coloured maculæ, and their surface presents delicate vesicular elevations, which are occasioned by the most matured ovisacs; the dehiscence of these takes place by minute punctiform openings in the peritoneal coat, and no cicatrix is left. At the period of puberty, the stroma of the ovaries is crowded with ovisacs; which are still so minute, that in the Ox (according to Dr. Barry's computation) a cubic inch would contain 200 *millions* of them. The greatest advance is seen in those which are situated nearest the surface of the Ovarium; and in such, the Graafian vesicle, with its two coats, may be distinctly traced. In those animals whose aptitude for conception is periodical, the development of the ova to such a degree that they become prepared for fecundation, is periodical also. This development is made evident when the parts are examined in an animal which is 'in heat,' by the projection of the Graafian vesicles from the surface (Fig. 314); and it consists not merely in an increase of size, but in certain internal changes presently to be described (§ 703).

Fig. 314.



Ovarium of the Rabbit, at the period of Heat; showing various stages of the extrusion of ova.

699. In the Human female, the period of *Puberty*, or commencing aptitude for procreation, is usually between the 13th and 16th years; it is generally thought to be somewhat earlier in warm climates than in cold;* and in densely-populated manufacturing towns than in thinly-peopled agricultural districts. The mental and bodily habits of the individual have also considerable influence upon the time of its occurrence; girls brought up in the midst of luxury or sensual indulgence undergoing this change earlier than those reared in hardihood and self-denial. The changes in which puberty consists are for the most part connected with the Reproductive system. The external and internal organs of generation undergo a considerable increase of size; the mammary glands enlarge; and a deposition of fat takes place in the mammæ and on the pubes, as well as over the whole surface of the body, giving to the person that roundness and fulness which are so attractive to the opposite sex at the period of commencing womanhood. The first appearance of the Catamenia usually occurs whilst these changes are in progress, and is a decided indication of the arrival of the period of puberty; but it is not unfrequently delayed much longer; and its absence is by no means to be

* It has been stated, by almost all physiological writers, that women (like fruits) reach maturity, and that menstruation commences, much earlier in hot climates, particularly between the tropics, than in temperate and very cold countries. From many elaborate and interesting papers which have been published within a few years, however, especially from those of Mr. Roberton of Manchester (collected in his "Essays on Menstruation, and on Practical Midwifery," 1851), it would seem that the natural period of puberty in temperate climates occurs in a much more extended range of ages, and is much more equally distributed through that range, than others have alleged; and that, in other countries, the supposed parallel between plants and fruits does not hold good. The fact seems to be that this, like other *periodic* phenomena of warm-blooded animals, is but little influenced by external temperature, simply because the rate of growth and development, of which these phenomena are the exponents, is determined by the temperature of the body itself, not by that of the surrounding medium. Still it is quite possible that external warmth may have a slight influence in determining early puberty; since, as already shown, it tends to maintain a somewhat higher degree of bodily heat (§ 396). According to Szukitz, the average age at which the catamenia appear amongst German women is 15½ years; according to Brierre de Boismont, it occurs a year earlier in Parisian girls. See Henle and Meissner's "Bericht," 1857, p. 606.

regarded as a proof of the want of aptitude for procreation, since many women have borne large families without having ever menstruated. The Catamenial discharge, as it issues from the uterus, appears to be nearly or quite identical with ordinary blood; but in its passage through the vagina, it becomes mixed with the acid mucus exuded from its walls, which usually deprives it of the power of coagulating. If the discharge should be profuse, however, a portion of its fibrin remains unaffected, and soft and diffluent clots are formed. In cases in which, by the death of women at this period, an opportunity has been afforded for the examination of the lining membrane of the uterus during menstruation, it is found to be unusually turgid with blood, the veins in particular being much distended, and opening upon the internal surface by capillary orifices, to which valvules are occasionally found attached.* Hence it is scarcely correct to designate the menstrual flux as a 'secretion;' although there is reason to think that it may carry off, besides blood, certain matters which would be appropriate to the formation of a Decidual membrane (§ 700), but which, if not so employed, become excrementitious.—The interval which usually elapses between the successive appearances of the discharge, is about four weeks; and the duration of the flow is from three to six days. There is great variety in this respect, however, among the inhabitants of different climates, and among individuals; in general, the appearance is more frequent, and the duration of the flow greater, among the residents in warm countries, and among individuals of luxurious habits and relaxed frame, than among the inhabitants of colder climes, or among individuals inured to bodily exertion. The first appearance of the discharge is usually preceded and accompanied by considerable general disturbance of the system, especially pain in the loins and a sense of fatigue in the lower extremities; and its periodical return is often attended with the like symptoms, which are more or less severe in different individuals.

700. Much discussion has taken place respecting the causes and purposes of the Menstrual flow; and modern inquiries have thrown great light upon them.† The state of the female generative system, during its continuance, appears to be analogous to the *heat* or periodic sexual excitement of the lower animals; some of which have a sero-sanguinolent discharge at that period, and among many of which the ova are entirely extruded by the female before the spermatic fluid of the male reaches them, this occasionally taking place even in Birds. There is good reason to believe that in the Human female the sexual feeling becomes stronger at the period of menstruation; and it is quite certain that there is a greater aptitude for Conception, immediately before and after the epoch, than there is at any intermediate period. Observations to this effect were made by Hippocrates, and were confirmed by Boerhaave and Haller; indeed, coitus immediately after menstruation appears to have been frequently recommended as a cure for sterility, and to have proved successful. This question has been made the subject of special inquiry by M. Raciborski; who affirms that the exceptions to the rule—that conception occurs immediately before or after, or during menstruation—are not more than 6 or 7 per cent. Indeed, in his latest work on the subject,‡ he gives the details of 15 cases, in which the date of conception could be accurately fixed, and the time of the last appearance of the catamenia was also known; and in all but one of them,

* See Whitehead "On Abortion and Sterility," pp. 13–37.

† For an excellent example of the absurd superstitions which still cling to the Menstrual period, and which will one day form an interesting and instructive chapter in Medicinal Folk Lore, see "The British Medical Journal," vol. ii. 1879, in which evidence is adduced from various sources to show that meat salted by a menstruating woman will certainly spoil.

‡ "Sur la Ponte des Mammifères," Paris, 1844. See also "Lancet," 1871, vol. i. p. 421.

the correspondence between the two periods was very close. Even in the exceptional case, the catamenia made their appearance shortly after the coitus, which took place at about the middle of the interval between the two regular periods. When conception occurs immediately before the menstrual period, the catamenia sometimes appear, and sometimes are absent; if they appear, their duration is generally less than usual. The fact that conception often takes place immediately *before* the last appearance of the catamenia (and not *after* it, as commonly imagined), is one well-known to practical men.—Numerous cases have been collected by Mr. Girdwood, Dr. Robert Lee, MM. Gendrin, Negrier, Raciborski, and others, in which the menstrual period was evidently connected with the maturation and discharge of the ova;* but the most complete observations yet made on the subject, are those of Dr. Ritchie (loc. cit.). He states that about the period of puberty a marked change usually takes place in the mode in which the ovisacs discharge their contents; but that this change does not necessarily occur simultaneously with the first appearance of the catamenia; as in some cases the conditions which obtain in the period before puberty, are extended into that of menstruation. The ovaries now receive a much larger supply of blood; the ovisacs show a great increase in bulk and vascularity, so that, when they appear at the surface of the ovary, they present themselves as pisiform turgid elevations; and the discharge of their contents leaves a much larger cicatrix, and is accompanied by an effusion of blood into their cavity, with other subsequent changes to be presently described. It would appear, however, that although such a discharge takes place *most frequently* at the menstrual period, yet the two occurrences are not necessarily co-existent; for menstruation may take place without any such rupture; whilst, on the other hand, the maturation and discharge of mature ova may occur in the intervals of menstruation, and even at periods of life when that function is not taking place. Perhaps the most correct general statement on the subject would be this: that there is a periodic return of Ovarian excitement, which *tends to* the maturation and extrusion of ovules, though it may not always reach that point; whilst there is also a periodic turgescence of the vessels of the lining membrane of the Uterus, which *tends to* the production of a decidual membrane;—but that these two periods, though usually coincident, are not necessarily so; and that either change *may* occur without the concurrence of the other. Thus removal of the ovaries, especially when the operation is performed before the age of puberty, is usually followed by arrest of the menses, though cases are on record in which menstruation occurred after extirpation of both ovaries.

701. The duration of the period of aptitude for procreation, as marked by the persistence of the Catamenia, is more limited in Women than in Men, usually terminating at about the 45th year; it is sometimes prolonged, however, for ten or even fifteen years further; but cases are rare in which women above 50 years of age have borne children. The time of the cessation of the flow is known as the Menopause; it occurs gradually, and with it are lost many of the peculiar sexual characteristics.† There is usually no menstrual flow

* Such, at least, appears to be the legitimate inference from the state of the Ovaries; but the cases are very few in which the extruded Ova have been found in the female passages. Two such cases (one of them, however, not altogether satisfactory) were recorded by Dr. Letheby in "Philos. Transact.," 1852.

† Dr. Matthews Duncan has clearly shown ("Trans. Roy. Soc. of Edin.," vol. xxiii. p. 186) that the total fertility of fertile women diminishes as the age at which marriage takes place increases. Sterility is rare amongst those marrying between the ages of 20 and 24, but about 7 per cent. of those marrying between 15 and 20 are sterile. These last, however, where fertile, bear more children than those marrying at a later date.

during pregnancy and lactation; in fact, the cessation of the catamenia is generally one of the first signs indicating that conception has taken place. But it is by no means uncommon for them to appear once or twice subsequently to conception; and in some women there is a regular monthly discharge, though probably not of the usual character, through the whole period. Some very anomalous cases are on record in which the catamenia never appeared at any other time than during pregnancy, and were then regular. The absence of the catamenia during lactation is by no means constant, especially if the period be prolonged, though as a rule they reappear about the tenth month; when the menstrual discharge occurs, it may be considered as indicating an aptitude for conception; and it is well-known that, although pregnancy seldom recurs during the continuance of lactation, the rule is by no means invariable. In women who do not suckle menstruation recurs within six weeks after confinement.

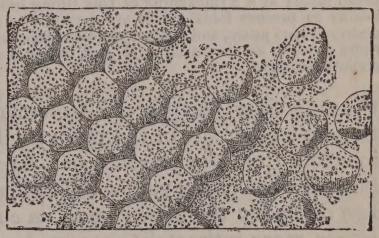
702. The function of the Female, during the coitus, is essentially passive. When the sexual feeling is strongly excited, there is a considerable degree of turgescence in the erectile tissue surrounding the vagina, and composing the greater part of the nymphæ and the clitoris; and there is an increased secretion from various glandular follicles.* But these changes are by no means necessary for effectual coition; since it is a fact well established, that fruitful intercourse may take place when the female is in a state of narcotism, of somnambulism, or even of profound ordinary sleep. It has been supposed by some that the os uteri dilates,† by a kind of reflex action, to receive the semen; but the introduction of a small quantity of the fluid just within the vagina, appears to be all that is absolutely necessary for conception; for there are many cases on record in which pregnancy has occurred, in spite of the closure of the entrance to the vagina by a strong membrane in which but a very small aperture existed. That the spermatozoa make their way towards the ovarium, and fecundate the ovum either before it entirely quits the ovisac or very shortly afterwards, appears to be the general rule in regard to the Mammalia; and their power of movement must obviously be both vigorous and long-continued to enable them to traverse so great an extent of mucous membrane, especially when it is remembered that they ascend in opposition to the direction of the ciliary movement of the epithelial cells, and to the downward peristaltic action of the Fallopian tubes, which may generally be noticed in animals killed soon after sexual intercourse.—We shall now consider the changes in the Ovum and its appendages, by which it is prepared for fecundation.

* The glands of Duverney or Bartholin, which were very accurately described by Professor Tiedemann (1840), and subsequently by M. Huguier in the "Archives d'Anatomie" (1847), seem to be analogous to Cowper's glands, and, like them, are sometimes wanting and differ in size. In advanced age they are said to diminish in size, and even to disappear. They are present in the females of all animals where Cowper's glands exist in the males, and are structurally large compound tubular mucous glands. They secrete a thick, tenacious, greyish-white fluid, which is emitted in large quantity at the termination of the sexual act, most likely from the spasmodic contraction of the constrictor vaginæ muscle, under which they lie. Its admixture with the male semen has been supposed to have some connexion with impregnation; but no proof whatever has been given that any such admixture is necessary. It seems not improbable, however, that it may serve, like the prostatic fluid of the male, to give a *dilution* to the seminal fluid that is favourable to its action (§ 690). These glands were probably known to the ancients; and it is doubtless their secretion which Hippocrates and others described as the female semen.

† See cases reported by Litzmann in 1846, and by Dr. J. R. Beck ("Med. and Surg. Reporter," 1872, No. 15), which seem to show that the uterus may participate rather actively in the process of impregnation. The latter observer noticed that the os uteri opened and closed with considerable energy on mechanical stimulation.

703. Up to the period when the Ovum is nearly brought to maturity, it remains in the centre of the ovisac or inner layer of the Graafian follicle; and it is supported in its place by the 'membrana granulosa,' which is continuous with its proligerous disk. The movement of the ovum towards the surface, which has been already referred to as a part of the changes by which it is prepared for fecundation, appears from the observations of Valentin to be due to the following cause:—In the immature ovisac, the space between its inner layer and the ovum is for the most part filled up with cells; these, however, gradually dissolve away, especially on the side nearest the surface of the ovary; whilst an albuminous fluid is effused from the deeper part of the ovisac, which pushes the residual layer (forming the discus proligerus) before it, and thus carries it against the opposite wall. At the same time, there is a gradual thinning away of the various envelopes of the Graafian follicle, as well as of its own walls, in the situation of its most projecting part; and thus it is preparing to give way at that point for the discharge of the contained ovum. Before rupture takes place, however, the ovisac itself undergoes a considerable change. Its walls become more vascular externally, and are thickened on their interior by the deposit of a fleshy-looking substance, which in many of the lower Mammalia is of a reddish colour, whilst in the Human female it is rather of a yellowish hue. This substance, known as the *Corpus luteum*, is at first entirely composed of an aggregation of cells (Fig. 315), and may, in fact, be considered as an increased development, or hypertrophy, of the 'membrana granulosa' or epithelial lining of the ovisac. Into this hypertrophied portion grow capillary blood-vessels, carrying with them migratory cells. The cavity of the follicle is thus gradually filled up with the hypertrophied epithelium, and the blood-vessels and pigment cells. The central portion becomes converted into gelatinous tissue, whilst the peripheral parts become hypertrophied and folded, the cells undergo fatty degeneration, the oil particles at first separate, ultimately coalesce, and press the nucleus to the side of the cell. In most domestic quadrupeds, this growth, which sprouts like a mass of granulations from the lining of the ovisac, is often so abundant, if the ovum be impregnated, as not only to fill the cavity of the ruptured vesicle, but even to protrude from the orifice on the surface of the ovary; this orifice subsequently closes, and the contained growth becomes gradually firmer, its colour changing from red to yellow. In the Human female, however, as in the Sow, this new formation is at first less abundant; it does not form mammillary projections from the interior of the ovisac, but lies as a uniform layer upon its lining; and this is thrown into wrinkles or folds, in consequence of the contraction of the ovisac (Fig. 316, *a*—*d*). An irregular cavity is thus at first left in the interior of the ovisac, after the discharge of the ovum; but this gradually diminishes, partly in consequence of the increased growth of the yellow substance, and partly owing to the general contraction of the ovisac, until it is at last nearly obliterated or reduced to a sort of stellate cicatrix (*e*—*h*). An effusion of blood usually takes place into this cavity, in the Human female, at the time of the rupture of the ovisac; but the coagulum which is left takes no share in the formation of the yellow body. It generally loses its colouring matter,

Fig. 315.

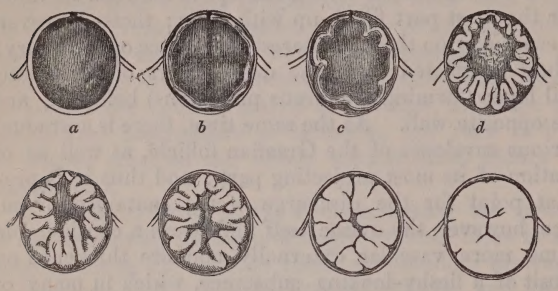


Cells forming the original substance of the *Corpus Luteum*.

and acquires the characters of a fibrinous clot; and this may either form a sort of membranous sac lining the cavity, or it may become a solid mass occupying the centre of the stellate cicatrix.*

704. The latter part of the history of the Corpus Luteum is greatly influenced by the impregnation or non-impregnation of the Ovum whose extrusion it has followed.—If conception do not take place, the corpus luteum seldom attains a size greater than that of a small pea, and is very commonly less than this; and it begins to diminish about the time of the next menstruation, its shape, which was at first globular, becoming somewhat collapsed and flattened. This diminution is due in the first instance to the absorption of part of its contained coagulum, which usually at the same time loses part of its colouring matter; but contemporaneously with this, there is an increase in the proper yellow substance, which also becomes brighter in colour from the presence of a large quantity of oleaginous matter in its cells. Soon, however, the yellow substance becomes softer and more friable, showing less distinctly the markings of its convolutions; whilst at the same time it becomes more intimately connected with the neighbouring tissues. The central coagulum becomes a faint, whitish, stellate cicatrix; and the yellow substance assumes various irregularities of form, and gradually decreases in size. As a general rule, the corpus luteum of the non-pregnant female is reduced within six or eight weeks to a very insignificant size; but it may then remain almost unchanged for many months: so that, in the ovaries of females who have menstruated regularly, numerous obsolete corpora lutea may be distinguished. —But if, on the other hand, the discharged ovum should be fertilized, and pregnancy should supervene, the corpus luteum instead of reaching its maximum of development in three or four weeks, and then undergoing atrophy, continues to develop itself for a considerable period, and does not, in fact, become very decidedly retrograde, until after the termination of gestation. This difference relates not only to its size, but also to its aspect and general characters. Its size appears to be usually greatest between the third and the sixth months of pregnancy; it retains its globular or only slightly flattened form; and it continues to give to the touch a sense of considerable resistance and solidity. The convoluted wall of yellow substance becomes much thicker in proportion to the space in its interior; so that whilst in the non-impregnated female its thickness never exceeds one-eighth of an inch, and is usually much less, that of the pregnant female measures as much as

FIG. 316.



Successive stages of the formation of the *Corpus Luteum* in the Graafian follicle of the Sow, as seen in vertical section: at *a* is shown the state of the follicle immediately after the expulsion of the ovum, its cavity being filled with blood, and no ostensible increase of its epithelial lining having yet taken place; at *b*, a thickening of this lining has become apparent; at *c*, it begins to present folds which are deepened at *d*, and the clot of blood is absorbed *pari passu*, and at the same time decolorized; a continuance of the same process, as shown at *e*, *f*, *g*, *h*, forms the Corpus Luteum, with its stellate cicatrix.

* This process was first accurately described by M. Pouchet, in his "Théorie Positive de l'Ovulation spontanée," 1847. See also Dr. Charles Creighton, 'A Theory on the Homology of the Supra-renals,' "Journal of Anatomy and Physiology," vol. xiii. (1879), p. 72.

from three-sixteenths to one-fourth of an inch. This substance, moreover, acquires a firmer and more highly organized structure; but instead of presenting an increased brightness of colour, it fades to a dusky and indefinite hue. As, from the time that impregnation takes place, the periodical activity of the ovary is suspended, no new vesicles protrude themselves from its surface until after the completion of gestation; and even those which, at the date of conception, happened to be more or less prominent, appear again to recede. Hence, if the period of pregnancy be at all advanced, the corpus luteum is not found, like that of menstruation, in company with unruptured vesicles in active process of development. After parturition, the corpus luteum rapidly diminishes; though its characteristic structure is still to be distinguished for many months, by close inspection.* Many Graafian follicles previous to the age of puberty undergo a similar process of degradation, but in no case is it then carried to so great an extent.†

705. The foregoing differences (whose ordinary existence may be considered as well established, although it may not be affirmed that they present themselves characteristically in each individual case) are probably to be attributed to the increased determination of blood which takes place to the whole generative apparatus, when it is in a state of exalted functional activity. It is a question, however, of much scientific interest, and one that occasionally becomes of importance in Juridical investigations, what degree of resemblance may exist between the corpus luteum which is formed after the mere extrusion of an ovule, and that which has been modified by the supervention of pregnancy. For it is unquestionable that an unusual development of the fibro-cellular substance may sometimes occur without impregnation; whilst, on the other hand, the changes which usually follow impregnation may take place so much less characteristically than usual, that the corpus luteum, even at the middle period of pregnancy, may be no larger than that which is often found where pregnancy has not occurred. These variations, which seem mainly to depend upon differences in the degree of vascular excitement of the ovaries accompanying and succeeding the extrusion of ova, render it impossible to draw any definite line of demarcation by which we may at once determine what are, and what are not, the results of conception; but the following practical rules, deduced from a consideration of all the circumstances yet known, may be laid down for the guidance of those who find it desirable to have some standard of judgment:—"1. A Corpus Luteum, in its earliest stage (that is, a large vesicle filled with coagulated blood, having a ruptured orifice, and a thin layer of yellow matter in its walls), affords no proof of impregnation having taken place.—2. From the presence of a Corpus Luteum, the opening of which is closed, and the cavity reduced or obliterated, only a stellate cicatrix remaining, and if the Corpus Luteum be of small size, not containing as much yellow substance as would form a mass the size of a small pea, no conclusion as to pregnancy having existed, or fecundation having occurred can be drawn.—3. A similar Corpus Luteum, of larger size than a common pea, would be strong presumptive evidence not only of impregnation having taken place, but of pregnancy having existed during several weeks at least; and the evidence would approximate more and

* See especially the Prize Essay of Dr. J. C. Dalton, 'On the Corpus Luteum of Menstruation and Pregnancy,' in the "Transact. of the American Medical Association" for 1851, and separately reprinted, Philadelphia, 1851; and the excellent section on 'Reproduction,' in his "Human Physiology," Philadelphia, 1864; also, the essay of M. His in Schultze's "Archiv," Band i. p. 181, in which references to the principal works on the subject will be found.

† De Sinéty, "Arch. de Physiol.," Aug. and Sept. 1875.

more to complete proof, in proportion as the size of the corpus luteum was greater."*

706. Since the discharge of matured Ova from the ovaries takes place as independently of sexual intercourse in the Human female (and in the Mammalia generally) as it does in those animals whose ova are fertilized out of the body, it seems unnecessary that the seminal fluid should reach the ovarium in order to effect the fertilization of the ova, since this end may be answered by the contact of the two in the Fallopian tubes, or even in the Uterus itself. From the experiments of Bischoff, however, it appears that in rabbits, bitches, and probably in most other Mammalia, sexual union usually takes place previously to the escape of the ova from the ovary, and that sufficient time often elapses for the seminal fluid to reach the ovary before their extrusion occurs: in such cases, therefore, it would seem probable that fecundation is effected at the ovary itself. That such occasionally happens in the Human female, seems to be unequivocally proved by the occurrence of tubal or even of ovarian fœtation; the ovum having received the fertilizing influence immediately upon quitting the ovisac, or even before it has entirely extricated itself from the ovary, and having been in some way checked in its transit towards the uterus, so that its development has taken place in the spot at which it has been arrested. It is affirmed by Bischoff that by the time the ovum reaches the uterus, or even the lower end of the Fallopian tube, its capacity for impregnation is lost; but this assertion chiefly rests on the cessation of sexual desire observed in those animals in which, after death, the ova were found in these situations. There is every reason to believe that this is not the case in the Human female; for although the sexual desire may be the strongest about the period of the maturation and escape of the ova, yet it is by no means wanting at other times; and the occasional occurrence of cases in which impregnation has taken place from a single coitus in the middle of the interval between the menstrual periods, shows either that the ovum may retain its capacity for impregnation for some time after its escape from the ovary, or that its maturation and extrusion are not by any means invariably coincident with the menstrual period.† The ova, when set free from the ovaries by the rupture of the ovisacs and the giving-way of their several envelopes, and surrounded by the cells of the discus proligerus, are received by the fimbriated extremities of the Fallopian tubes, which, during the period of sexual excitement, appear to be closely applied to the surface of the ovaries. Their conveyance along the Fallopian tubes is probably due in part to the peristaltic movement of their walls, and in part to the action of the cilia which clothe their internal surface.

707. The object of the changes which have been already described, is to bring the Ovum within the reach of the fecundating influence, and to convey it into the uterus after it has been fertilized; we have now to consider the changes of the Ovum itself, which take place during the same epoch. Special attention has been devoted during the last few years by various observers‡ to

* See Dr. Baly's "Supplement to Müller's Physiology," p. 57.

† See a case of this kind recorded by Dr. Oldham in the "Medical Gazette," July 13, 1849.—Instances are certainly not unfrequent, in which conception has taken place five or six days after the conclusion of the menstrual period; the Author has himself known one in which this occurred, after the menstrual flow itself had persisted for a week. It has been urged that the known fertility of Jewish females, who abstain from sexual intercourse for eight days, or even thirteen days, after the termination of the catamenia, is opposed to the idea that the menstrual period is that of 'heat;' but there is reason to believe that this is to be accounted for in another way—namely, by the usual occurrence of conception from intercourse immediately *before* the access of the catamenia. (See Mr. Girdwood, in the "Lancet," Dec. 14, 1844.)

‡ Accounts of the recent investigations in regard to the changes taking place in the ovum

the observation of certain phenomena presented by the ovum previous to and immediately succeeding its impregnation. The researches have been carried on for the most part with the eggs of the rabbit amongst Mammalia; and of Asterias, and certain of the Vermes amongst the Invertebrata, but there appears reason to suppose that the results thus obtained hold good for ova generally. Previous to fertilization, when the ovum is mature, but in the majority of cases before it has left the ovary, the germinal vesicle which occupied a central position moves towards the periphery of the yolk; it always takes up its position at the precise point of the zona pellucida, which is nearest the ovisac, and which is therefore closest to the surface of the ovary. The membrane surrounding the germinal vesicle is then absorbed, the germinal spot is broken up and disappears, and a portion of the vesicle itself seems to undergo absorption. The remainder of the germinal vesicle elongates (Fig. 327, *a*), and is converted into a spindle-shaped body (*b*), of which the middle portion is striated longitudinally, each of the striæ presenting about its centre a thickened portion composed of fine granules (*c*). The spindle then travels to the surface of the ovum where it divides into two portions; one lying in the space between the ovum and its surrounding membrane, and giving rise to the polar bodies: a second remaining within the egg and forming after division and subsequent aggregation the *female pronucleus*. The extrusion of the polar bodies or directive corpuscles generally occurs in the case of rabbits just after the ovum has entered the Fallopian tube. Spermatozoa coming in contact by their heads with the ovum at this period, become enveloped in the surrounding mucilaginous coat. A prominence from the protoplasm of the egg is put out until it reaches the nearest spermatozoon, which then makes its way into the egg through the projecting portion. The head alone of the spermatozoon appears to enter the egg, the tail, which remains visible for some time on the exterior, ultimately undergoes certain changes and disappears, apparently owing to its fusion with the protoplasm of the egg. At the instant of contact of the spermatozoon with the egg, the most external layer of protoplasm separates itself and forms a membrane, thereby preventing the entrance of more spermatozoa. The head which has thus entered forms the male pronucleus, it grows in size, whilst the protoplasm immediately surrounding it assumes a radiating arrangement. *The male pronucleus* thus formed travels towards the female pronucleus, with which it ultimately coalesces to produce the first segmentation nucleus, the subsequent changes in which will be presently noticed (§ 734). Commenting upon these phenomena, Mr. Balfour observes,* "that the act of impregnation is seen to consist essentially in the fusion of the male and female nucleus: not only does this appear in the actual fusion of the two pronuclei, but it is brought into still greater prominence by the fact that the female pronucleus is a product of the nucleus of a primitive ovum, and the male pronucleus is the metamorphosed *head* of the spermatozoon, which is itself developed from the nucleus of a spermatic cell. The spermatic cells originate from cells identical with the primitive ova, so that the fusion which takes place is the fusion of morphologically similar parts in the two sexes."† In the Osseous Fishes it has been shown by Dr.

previous to fertilization may be read in Oellacher, "Archiv f. Mikros. Anat." viii. p. 24; Prof. Van Beneden's Paper, "Quarterly Journ. Microscop. Sci." vol. xvi. (1876), p. 153; and in Summaries by Priestley, *ib.* p. 130; and Balfour, *ib.* vol. xviii. p. 108. In each paper full bibliographies will be found.

* Op. cit. vol. xviii. p. 129.

† The results of Newport's experiments upon the fertilization of ova will be found in the "Philosoph. Trans.," 1851, p. 178, and 1853, pp. 266–281. See also Huxley on the 'Development of Pyrosoma,' "Linn. Trans.," vol. xxiii. p. 227, and "Ann. Nat. Hist.," ser. 3, vol. v. pp. 29–35. See also Dr. Barry, in "Philosoph. Transact.," 1840, p. 533; and Dr. Ransome, in

Ransom that the spermatozoa pass through a minute opening in the external membrane of the ova, termed the *micropyle*. A similar opening has been observed by Müller and others in Insects, Acephalous Mollusks, and in several Echinodermata; and its use, as Dr. Allen Thompson has suggested, is probably to facilitate the fecundation of ova possessed of very thick external coverings. A micropyle has not been seen in any of the Mammalia, though the point has been closely investigated by Reichert in the Guinea Pig. It has been remarked by Mr. Newport, that spermatozoa whose spontaneous *motility* has ceased, no longer possess the fecundating power; and this fact concurs with other phenomena to indicate, that it is not only a certain *material*, but a *vital force* of which that material is (so to speak) the vehicle, which is required to effect this most important operation.

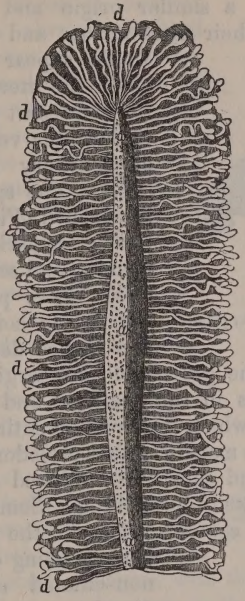
708. Having thus noticed the principal points of the history of the development and impregnation of the Ovum, we shall proceed to consider the provisions made for the Nutrition of the Embryo, through the generative apparatus of its female Parent, up to the time of parturition; deferring the history of its own Development for that separate consideration which the importance of this subject demands (Sect. 4).—About the time that the ovum is leaving the ovary, the cells of the proligerous disk which immediately surrounds the zona pellucida become club-shaped; their small ends being applied to the surface of the ovum, so as to give it somewhat of a stellate appearance. According to Bischoff, these cells entirely disappear from the ovum of the Rabbit as soon as it has entered the Fallopian tube: whilst in the Bitch they become round, and continue to invest the ovum in this form throughout its whole transit to the uterus. During its passage, the ovum acquires a sort of gelatinous envelope, which is enclosed in a membrane of fibrous tissue, termed the *Chorion*. This envelope is probably of an *albuminous* nature, corresponding with the 'white' of the Bird's egg; whilst the fibrous texture of the chorion seems to be produced, like the membranous basis of the egg-shell of the bird, by the exudation of fibrin from the lining membrane of the Fallopian tube or oviduct. The outer layer of this envelope, in the egg of the Bird, is consolidated by the deposition of particles of carbonate of lime in its areola; and none of it undergoes any further organization. The Chorion of the Mammal, on the other hand, is destined to undergo changes of a much higher order, which adapt it for participating to a most important degree in the nutrition of the included embryo. The first of these changes consists in the extension of the cellular surface of the membrane into a number of villous prolongations, which give it a spongy or shaggy appearance (Fig. 321). These processes are very largely developed in the human ovum, and form the *chorion frondosum;* they serve as absorbing radicles, and act as the channels through which the embryo is nourished by the fluids of the parent,

"Proceed. of Roy. Soc.," Nov. 23, 1854. Bischoff (Henle and Pfeuffer's "Zeits.," 1865, p. 268) considers that, in the majority of cases, the act of fecundation occurs whilst the ovum is traversing the Fallopian tube. According to Coste, the duration of the passage of the egg through the oviduct of the fowl varies from four to six hours, and of its retention in the cloaca four hours; whilst Foster & Balfour ("Elements of Embryology," p. 21) state that it remains in the oviduct for a period of 24 hours. The influence of a single act of coition in the fowl, according to the same observer, may extend to from five to six eggs, which may be laid during the eleven to seventeen subsequent days. Harvey extended the influence even to twenty eggs. His agrees with Coste, and observes, that in all probability these eggs were impregnated at different periods: and hence may proceed some of the variations in point of development of the cicatricula. His has also observed that the eggs of fowl, laid in the middle of summer, are more advanced, and develop with greater rapidity than those laid towards the end of autumn

until a more perfect communication is formed by the subsequent extension of vessels into them.

709. We have now to speak of the changes in the Uterus which take place in consequence of Conception, and which prepare it to receive the ovum.* Of these the most important is the formation of the *Membrana Decidua*, so called because the greater portion of it is cast-off at each parturition. Professor Turner has pointed out that as soon as the ovum is received into the uterus, the mucous membrane swells; and there is reason to suppose that certain changes, closely resembling those which take place at each menstrual period, are set up in the uterus before the ovum reaches it. Thus the ciliated *epithelium* often, though not always, loses its columnar form, and the cells multiply in order to cover the increased surface. The *submucous tissue* increases enormously, which is due to the multiplication and development of the corpuscles which are abundantly distributed through its tissue. The *branched glands* naturally present, as seen in vertical sections, are separated to a much greater distance from each other in consequence of the growth of the sub-epithelial tissue, and are augmented in size. The whole membrane becomes much more vascular. On its surface pit-like depressions may be seen, which were formerly thought to be the enlarged mouths of the glands, but which Professor Turner has ascertained to be new-formed pits or *crypts in the interglandular tissue*. Into these crypts the villi of the chorion penetrate. During menstruation the thickness of the mucous membrane is increased as above described; but by a retrogressive process the epithelium and the greater part of the glands and mucous membrane then undergo a fatty degeneration and are finally detached. If, however, the ovum which is discharged at this period be fecundated, these changes do not pass into the retrograde stage, but advance to the hypertrophy which gives rise to the decidua.

Fig. 317. Fig. 318.



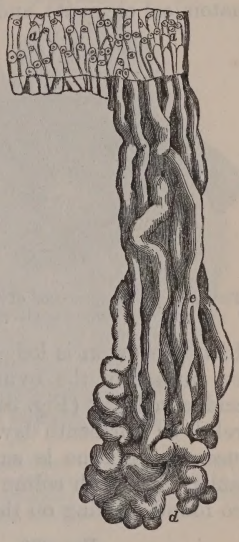


Fig. 317. Section of the *Lining Membrane of a Human Uterus* at the period of commencing pregnancy, twice the natural size; showing the arrangement and other peculiarities of the glands *d*, *d*, *d*, with their orifices *a*, *a*, *a*, on the internal surface of the organ.

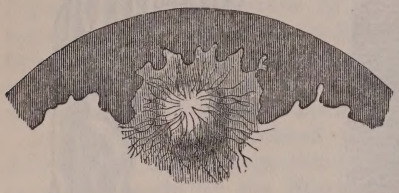
Fig. 318. A portion of Fig. 317 more enlarged, showing the convoluted extremities of the tubular glandulæ.

710. The Deciduous membrane is found at a later period to consist of two

* See Williams, 'On the Structure of the Uterine Mucous Membrane,' "Obstet. Journal," 1875, Nos. 23 and 24.

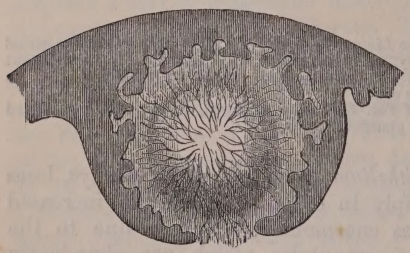
layers: the *Decidua vera* lining the uterus, and the *Decidua reflexa* covering the exterior of the ovum. The observations of M. Coste, Dr. Farre and De Sinéty* show that there is considerable resemblance between the two at an early period, since they have a similar origin and consist of the same anatomical elements, and from their observations and those of Reichert,† it would appear that when the ovum enters the uterus, it becomes attached to some part of a triangular area of the decidua vera, on which numerous cotyledonary elevations or islands exist. The spot at which the ovum is attached (Fig. 319) ceases to grow, but a remarkable development of primary and secondary papillary processes takes place in the adjoining islands, in consequence of which a cup-shaped depression is formed, in which the ovum is lodged. The growth of the margin of the cup over the free surface of the ovum, closes in the chamber and forms the membrana decidua reflexa‡ (Fig. 320), by which the ovum is entirely covered about the twelfth or thirteenth day. At the margin of the cotyledonary island, the uterine mucous membrane is smooth and shows the widened orifices of the uterine glands, lined with columnar ciliated epithelium. Some utricular glands are also found opening on the inner concave surface of the reflexa, the rest of the surface being covered with a short, non-ciliated cylindrical epithelium. As the ovum increases in size, the cavity between the decidua vera and the decidua reflexa, or, as it is sometimes termed, the uterine chamber, which communicates by its superior angles with the Fallopian tubes, and below with the canal of the cervix, gradually diminishes, and by the end of the third month either the two layers come into contact and are henceforth indistinguishable—the whole cavity of the uterus being occupied by the fœtal chamber—or, as Dr. Farre suggests, the decidua reflexa may, after first becoming extremely attenuated, ultimately entirely vanish. De Sinéty§ shows that to the end of pregnancy, remains of the uterine glands lined with columnar epithelium may be found in certain parts of the cavity of the uterus; after delivery, however, no epithelium can be discovered, but in its place are a number of cells presenting embryonal characters, which infiltrate the whole tissue. That portion of the decidua vera in which the chorionic tufts are embedded, and which afterwards forms the maternal portion of the placenta, is termed the *Decidua Serotina;* the greater portion of it is deciduous at parturition.

Fig. 319.



First stage of the formation of the *Decidua reflexa* around the Ovum.

Fig. 320.



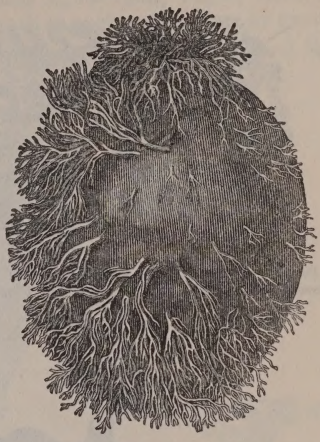
More advanced stage of the *Decidua reflexa.*

711. The surface of the Ovum, thus surrounded by the double layer of the deciduous membrane, and during the first three or four weeks lying loose in the fœtal chamber, is rendered shaggy by the growth of villous tufts from the

* "Archiv de Physiol," 1876, p. 342. † Reichert's "Archiv," 1873, p. 127.
‡ See 'Turner's Report,' "Journal of Anatomy and Physiology," vol. viii. p. 168.
§ Loc. cit.

surface of its investing Chorion (Fig. 321), by which it begins to be attached to the walls that surround it. Each of these tufts, as was first pointed out by Prof. Goodsir (loc. cit.), is composed of an assemblage of nucleated cells, which are found in various stages of development; and these are always enclosed within a layer of basement-membrane, which seems to be itself composed of flattened cells united by their edges.* At the free extremity of each villus is a bulbous expansion, the cells composing which are arranged round a central spot; and it is at this point that the most active processes of growth take place, the villus elongating by the development of new cells from its germinal spot, and (like the spongiole of the plant) drawing in nutriment from the soil in which it is imbedded. —In its earliest grade of development, the chorion and its villi contain no vessels; and the fluid drawn in by the tufts is communicated to the embryo by the absorbing powers of the germinal membrane of the latter. But when the tufts are penetrated by blood-vessels, an event which occurs about the third or fourth week according to Kölliker,† and their communication with the embryo becomes more direct, the means by which they communicate with the parent are found to be still essentially the same; namely, a double layer of nucleated cells, one layer belonging to the fœtal tuft, and the other to the vascular maternal surface. It is from these elements that the *Placenta* is formed.‡

Fig. 321.



Entire *Human Ovum* of eighth week, sixteen lines in length (not reckoning the tufts); the surface of the Chorion partly smooth, and partly rendered shaggy by the growth of tufts.

712. The first stage in this process consists in the extension of the Fœtal vessels into the villi of the Chorion over its entire surface, in the manner hereafter to be detailed; so that the nutriment which these villi imbibe, instead of being merely added to the albuminous fluid surrounding the yolk-bag, is now conveyed directly to the embryo. This—the earliest and simplest mode by which the Fœtus effects a new connection with the parent—is the only one in which it ever takes place in the lower Mammalia, which are hence properly designated as 'non-placental,' rather than as ovo-viviparous. In the higher Mammalia, however, there soon occurs a great extension of the vascular tufts of the fœtal chorion, at certain points; and a corresponding adaptation, on the part of the uterine structure, to afford them an increased supply of nutritious fluid. These specially prolonged portions are scattered in the Ruminantia and some other Mammalia, over the whole surface of the chorion, forming what are termed the 'cotyledons;' but in the higher orders, and in Man,

* Kölliker, "Entwickelungsgesch. des Mensch.," 1879, p. 334. † Loc. cit., p. 367.

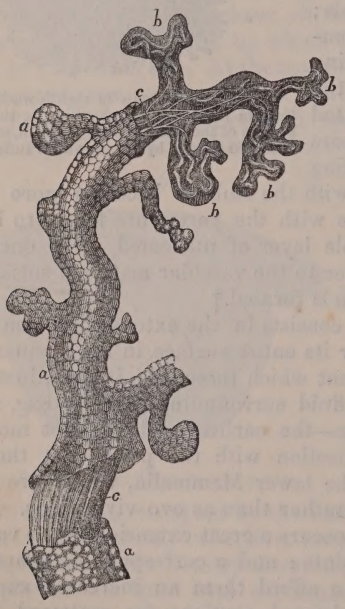
‡ The Placenta varies in form to a considerable extent in different animals. In Cetacea and in many Ungulata, as the Llama, Horse and Zebra, the villi project from all parts of the chorion, and their placenta is consequently termed *diffuse*. In Carnivora, in Seals, in the Elephant and Hyrax, the villi are only developed in a ring or zone around the chorion, and the placenta is therefore called *zonary*. In Ruminants the villi are developed in certain spots, irregularly distributed over the chorion, forming the *cotyledonous* placenta. Finally, in Man and in Rodents the villi are limited to a single spot, and the Placenta is thence termed *discoid*. See report of Turner's Lectures delivered at the College of Surgeons in "Lancet" for June, 1875, and in "Journal of Anat. and Physiol.," vol. x. p. 127.

they are concentrated in one spot, forming the Placenta. In some of the lower tribes the maternal and the fœtal portions of the placenta may be very easily separated; the former consisting of the thickened Decidua, and the latter being composed of the prolonged and ramifying vascular tufts of the Chorion, dipping down into it. But in the Human placenta the two elements are mingled together through its whole substance.—On looking at the fœtal surface of the Human placenta, we perceive that the umbilical vessels diverge in every direction from the point at which they enter it; and their subdivisions form a large mass of capillaries, arranged in a peculiar manner (Figs. 322, 323), and constituting what is known as the *fœtal villi*. Each villus contains one or more capillary loops, communicating with an artery on one side, and with a vein on the other: but the same capillary may pass into several villi, before re-entering a larger vessel. The capillaries of the villi are covered, as in the chorion, by a layer of cells (Fig. 323, *a*, *a*; Fig. 324, *e*), enclosed in a basement-membrane; but the fœtal tuft thus formed is enclosed in a second series of envelopes (Fig. 324, *a*, *c*, *e*), derived from the maternal portion of the placenta —a space (*ips*) being left, however, between the two, at the extremity of the tuft.

Fig. 322.

Portion of the ultimate ramifications of the umbilical vessels, forming the *Fœtal Villi of the Placenta.*

Fig. 323.



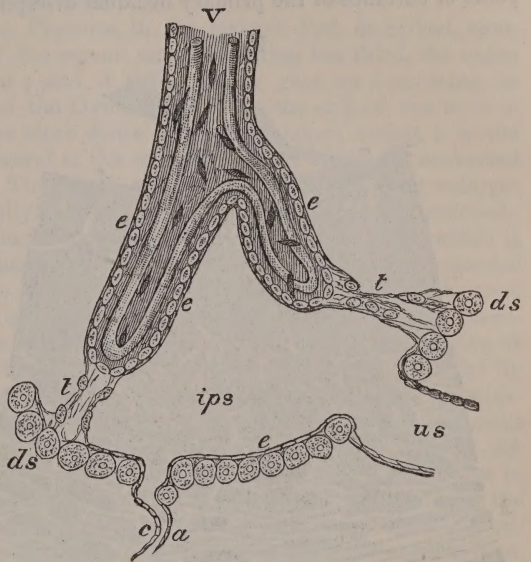
Portion of one of the *Fœtal Villi*, about to form part of the Placenta, highly magnified:—*a a*, its cellular covering; *b*, *b*, *b*, its looped vessels; *c*, *c*, its basis of connective tissue.

713. Whilst the *fœtal* portion of the Placenta is thus being generated by the extension of the vascular tufts of the Chorion, the maternal portion is formed by the enlargement of the vessels of the Decidua, between which they dip down. "These vessels assume the character of sinuses; and at last swell out (so to speak) around and between the villi; so that finally the villi are completely bound up or covered by the membrane which constitutes the walls of the vessels, this membrane following the contour of all the villi, and even passing to a certain extent over the branches and stems of the tufts. Between this membrane, or wall of the enlarged decidual vessels, and the internal membrane of the villi, there still remains a layer of the cells of the decidua."* In

* Prof. Goodsir's "Anatomical and Pathological Observations," p. 60. Prof. Turner "Journ. of Anat. and Physiology," 1873, p. 130) has recently demonstrated, however, that

this manner is formed the *maternal* portion of the placenta, which may be regarded in its adult state (as was well pointed out by Dr. J. Reid*) in the light of a large sac formed by a prolongation of the inner coat of uterine vessels; against the fœtal surface of which sac the tufts just described may be said to push themselves, so as to dip down into it, carrying before them a portion of its thin wall, which constitutes a sheath to each tuft. Now as every extension of the uterine vessels carries the decidua before it, every one of the vascular tufts that dips down into it will be covered with a layer of the cellular structure of the latter; and the fœtal portion of each tuft will thus during the earlier periods of intra-uterine life be generally enclosed in a layer of *maternal* cells and basement membrane (Fig. 323, *a*, *b*, *c*).† From observations made by Kölliker it appears that the fœtal villi are not in direct connection with the uterine glands, which soon shrink and disappear, but lie in the substance of the decidua in inter-glandular spaces. Reichert, however, states that he has seen the villi enter the mouths of the glands. The whole interior of the Placental cavity soon becomes (Fig. 325) intersected by numerous tufts of fœtal vessels disposed in fringes, and bound down by reflexions of the delicate membrane that forms its proper wall; just as the intestines are held in their places by the reflexions of the peritoneum that covers them. This view was suggested to Dr. Reid by the very interesting fact, that the tufts of fœtal vessels not unfrequently extend beyond the uterine surface of the placenta, and dip down into the uterine sinuses, where they are still covered and held in their places by reflexions of the same membrane. All the bands which connect and tie down the tufts are formed of the same elements as the envelopes of the tufts themselves; namely a fold of the lining membrane of the decidual sinuses, and a layer of the cellular decidua.

Fig. 324.



V, Placental Villus, consisting of gelatinous connective tissue with corpuscles; in its interior are seen the fœtal blood-vessels forming loops; *e*, *e*, epithelium investing the Villus, beneath which is a layer of cells forming the occluding lamina; *d s*, decidua serotina; *c*, *a*, curling artery; *u s*, uterine sinus; *t*, *t*, trabecula; *ips*, intra-placental maternal blood sinus.

the *decidua serotina* does not form a complete and continuous membranous septum between the uterus and placenta, but that its continuity is in various localities interrupted to allow of the penetration of many of the placental villi into the utero-placental vessels, into which they project free and naked.

* "Edin. Med. and Surg. Journ.," Jan. 1841; and "Anat., Phys., and Pathol. Researches," chap. viii.

† See Turner, 'Observations on the Structure of the Human Placenta,' in Humphry and Turner's "Journal of Anatomy and Physiology," vol. vii. 1873, p. 120, in which the literature of the subject will be found. See also Masquelin and Swaen 'Premières phases du développement du Placenta maternel chez le lapin,' "Archiv. de Biologie" (1880), tom. i. pp. 25–44.

714. The Maternal blood is conveyed into the Placental cavity by the 'curling arterics' of the uterus (Fig. 324, *c*, *a*, Fig. 325 *d*); and is received back from it into the large veins that are commonly designated as sinuses (Fig. 325, *b*, *b*). "The utero-placental sinus-system of veins is so related to the placenta as to communicate with the interior of the cotyledons, either at the outer edge of the placenta, where the so-called circular sinus lies, or where the sinuses lie within the inter-cotyledonary decidual dissepiments, or where they come into contact with the uterine face of the placenta, close to the plane of entrance of the primary decidual dissepiments into its substance. The communication is not as if the sinuses terminated abruptly by open mouths, as has already been described, but rather by possessing cribriform apertures in their walls as they lie in contact with the placenta. From the relation of the sinuses to the margins of the cotyledons, whilst the curling arteries penetrate their uterine surface near their centre, the stream of maternal blood passes through each cotyledon from its centre to its circumference, and is effectually brought into contact with the whole of the fœtal villi." The fœtal vessels (Fig. 324, *e*, *e*; Fig. 325, *c*, *c*) being bathed in this blood, as the branchiæ of aquatic animals are in the water that surrounds them, not only enable the fœtal blood to exchange its venous character for the arterial, by parting with its carbonic acid to the maternal blood, and receiving oxygen from it; but they also serve as rootlets, by which certain nutritious elements of the maternal blood (probably those composing the liquor sanguinis) are taken into the system of the fœtus. In this, they closely correspond with the villi of the intestinal canal; and there is this further very striking analogy—that the nutrient material is selected and prepared by two sets of cells, one of which (the maternal) transmits it to the other (the fœtal), in the same manner as the epithelial cells of the intestinal villi seem to take up and prepare the nutrient matter, which is destined to be still further assimilated by the cells that float in the circulating current. It is probable, too, that the Placenta is to be regarded as an excreting organ; serving for the removal, through the maternal blood, of excrementitious matter whose continued circulation through the blood of the fœtus would be prejudicial to the latter. And it will be in this mode that the blood of the mother may become impregnated with substances, or impressed

Fig. 325.

Section of a portion of a fully-formed *Placenta*, with the part of the Uterus to which it is attached:—*a*, umbilical cord; *b*, *b*, section of uterus, showing the venous sinuses; *c*, *c*, *c*, branches of the umbilical vessels; *d*, *d*, curling arteries of the uterus.

with attributes, originally belonging to the male parent; so as to impart these to the products of subsequent conceptions by a different father.* There is no more direct communication between the mother and fœtus than that which is afforded by this immersion of the fœtal tufts in the maternal blood; all the observations which have been supposed to prove the existence of real vascular continuity, having been falsified by the extravasation of fluid, probably consequent upon the force used in injecting the vessels. Moreover, the different size of the blood corpuscles in the fœtus and in the parent shows the non-existence of any such communication.

715. The formation of the Placenta, in the manner just described, commences in the latter part of the second month; during the third, the organ acquires its proper character; and it subsequently goes on increasing, in accordance with the growth of the Ovum. Towards the end of the term of gestation, however, it becomes more dense and less vascular; owing, it would seem, to the obliteration of several of the minuter vessels, which are converted into hard fibrous filaments. The vessels of the Uterus undergo great enlargement throughout, but especially at the part to which the placenta is attached; and the blood in moving through them produces a peculiar murmur, which is usually distinctly audible at an early period of pregnancy, and may be regarded (when due care is taken to avoid sources of fallacy) as one of its most unequivocal positive signs. The 'placental bruit' is thus described by Dr. Montgomery:†—"The characters of this phenomenon are, a low murmuring or somewhat cooing sound, resembling that made by blowing gently over the lip of a wide-mouthed phial, and accompanied by a slight rushing noise, but without any sensation of impulse. The sound is, in its return, exactly synchronous with the pulse of the mother at the time of examination; and varies in the frequency of its repetitions, with any accidental variation which may occur in the maternal circulation. Its situation does not vary during the course of the same pregnancy; but in whatever region of the uterus it is first heard, it will in future be found, if recognized at all—for it is liable to intermissions—at least, we shall occasionally be unable to hear it where we have already heard it a short time before, and where we shall shortly again recognize it. According to my experience, it will be most frequently heard about the situation of the Fallopian tube of the right side; but it may be detected in any of the lateral or anterior parts of the uterus." That the cause of this sound exists in the Uterus itself, is distinctly proved by the fact, that it has been heard when that organ was so completely *anteverted*, that the fundus hung down between the patient's thighs. A sound so much resembling this as to be scarcely distinguishable from it, may be occasioned, however, by a cause of a very different nature—namely, an abdominal tumour, pressing upon the aorta, iliac arteries, or enlarged vessels of its own; and, in doubtful cases, it is necessary to give full weight to the possibility of such an explanation. The sound may be imitated at any time by pressing the stethoscope on the iliac arteries. The placental bruit has not unfrequently been heard in the eleventh week; but it cannot generally be detected before the fourth month, when the fundus uteri rises above the anterior wall of the pelvis.

716. The increase in the size of the Uterus, which takes place *pari passu* with the enlargement of the ovum, is accompanied by a remarkable augmentation in the amount of its substance. Up to about the fifth or sixth month,

* See, for various proofs that the mother may be *poisoned* through the presence of noxious substances in the blood of the fœtus, the Essay by Mr. Savory, entitled "An Experimental Enquiry into the Effect upon the Mother of Poisoning the Fœtus," London, 1858.

† "Signs of Pregnancy," p. 121.

not only its cavity, but the thickness of its walls, is progressively added to; from that time, to the end of gestation, the thickness of the walls diminishes whilst the cavity increases, but not in an equal proportion; and at the conclusion of parturition, its solid bulk is estimated at about twenty-four times that of the unimpregnated Uterus. The augmented volume of the organ is chiefly due to the increased development of its Muscular coat, which is composed of the fusiform cells with staff-shaped nuclei, that make up the 'non-striated' muscular fibre elsewhere. According to Prof. Kölliker, a vast amount of new fibres are generated during the early months of pregnancy; but there is at the same time an extraordinary increase in the size of those previously formed, their length being multiplied from seven to eleven times, and their width from twice to five times. After the sixth month the origination of new muscular fibres seems to cease, but the augmentation in the size of those already generated seems to continue. The connective tissue which unites the bundles of muscular fibres into plexuses, and which is very scanty in the unimpregnated uterus, also increases during pregnancy, and becomes more distinctly fibrous.*

717. *Innervation of the Uterus.*—The uterus receives its motor fibres from two sources, from the hypogastric nerves issuing from the posterior mesenteric ganglion, and also from nerves issuing from the sacral plexus. An antagonistic action appears to exist between these two sets of nerves.† If the Hypogastric branches be electrically stimulated, contractions of the circular fibres of the uterus takes place, the cervix descending into the vagina whilst the os opens. On the other hand, on stimulation of the sacral nerves, the longitudinal fibres are made to contract, the uterus becomes shorter and the os remains closed. Suppression of the respiration, or stimulation of the sciatic nerve, acts in a reflex manner, chiefly on the hypogastric nerves. The vessels of the uterus obtain their nerves from the same sources as the muscular tissue; the nervi hypogastrici supplying the constricting, and the sacral nerves the dilating fibres, which last can also be brought reflectorially into action through the sciatics. The nerves entering the mucous membrane are connected with ganglia. According to Lindgren,‡ the mucous membrane contains a rich plexus of medullated fibres, which near the epithelium of the free surface gives off bundles of very fine fibrils. It has been shown by Dr. Lee,§ in his beautiful preparations and drawings, that the Nerves of the Uterus, as well as the blood-vessels and lymphatics,‖ undergo a great augmentation during pregnancy. Simultaneously with the enlargement of the uterus, the Mammary gland and its appendages undergo a fuller development; and from this a valuable, but not unequivocal, indication of pregnancy may be drawn. Occasional shooting pains in the Mammæ are not unfrequently experienced within a short period after conception; and more continued tenderness is also not unusual. A sense of distension is very commonly experienced at about the end of the second month; and from that time a distinct 'knottiness' usually begins to present itself, increasing with the advance of pregnancy. In many instances, however, these mammary sympathies are entirely absent; and they may be simulated by changes that take place in consequence of

* See Kölliker's "Manual" (Syd. Soc. Ed.), vol. ii. pp. 258, 259.

† v. Basch and Hoffmann, "Wien Med. Jahrb.," 1878.

‡ Klein and Noble Smith's "Atlas of Histology," 1880, p. 298.

§ "Phil. Transact." 1841, 1842, 1846, 1849.

‖ Körner, Heidenhain's "Stud. des Physiol. Instit. zu Breslau," 1865, p. 109. For the 'Histology of the Virgin Uterus,' see Kreitzen, in Landzert's "Beiträge zur Anat. and Phys.," St. Petersburgh, 1872, vol. i. p. 1; "Centralblatt," 1873, p. 117; and Klein and Noble Smith's "Atlas of Histology," 1880, pp. 294–298.

various affections of the uterus. A change of colour in the areola is a very common, but not an invariable, occurrence in the early months of pregnancy; but another sign is afforded by the areola and nipple, which is of more value because more constant—namely, a puffy turgescence, and an increased development of the little glandular follicles, or tubercles, which commonly secrete a dewy moisture.—Many other changes in the constitution occur during pregnancy, indicated by the buffiness of the blood, the irritability of the stomach, and the increased excitability of the mind. All these, however, are discussed with sufficient amplification in works on Obstetric Medicine.

718. The act of Conception, being one of a purely organic nature, is not itself productive of any sensation on the part of the mother; but there are some women in whom it is attended with certain sympathetic affections, such as faintness, vertigo, &c., that enable them to fix upon the particular time at which it has taken place. From that period, however, the mother has no direct consciousness of the change going on in the uterus (save by the effects of its increasing pressure on other parts), until the occurrence of what is termed 'quickening.' This is generally described as a kind of fluttering movement, attended with some degree of syncope or vertigo. After it has once occurred, and has strongly excited attention, it is occasionally renewed once or twice, and then gives place to the ordinary movements of the fœtus. Not unfrequently, however, no movement whatever is felt, until near the end of the term of gestation, or even through the whole of it. As to the cause of the Sensation, Obstetricians are much divided; and no satisfactory account has been given of it. It has been vulgarly supposed to be due to the first movement of the fœtus, which was imagined then to become possessed of an independent life; and the English law recognizes the truth of this doctrine, in varying the punishment of an attempt to procure Abortion, according to whether the woman be 'quick with child' or not; and in delaying execution when a woman can be proved to be so, though it is made to proceed if she is not, even if she be unquestionably pregnant. Whether or not the first *sensible* motions of the fœtus are the cause of the peculiar feeling in question, there can be no doubt that the embryo has as much independent vitality before, as after, the quickening. From the time that the ovum quits the ovary, it ceases to be a part of the parent, and is dependent on her only for a due supply of nourishment, which it converts by its own inherent powers into its proper fabric. But this dependence cannot be said to cease at the moment of quickening; for the connection must be prolonged during several weeks, before the fœtus becomes capable of sustaining life without such assistance. The earliest period at which this may occur, will be presently considered (§ 723).*

719. At the conclusion of about forty weeks or (less correctly) nine solar months,† from the period of conception, the time of Parturition arrives. In

* Oser and Schlesinger (Stricker's "Med. Jahrb.," 1872) have shown that powerful contractions of the uterus are produced by the circulation of dyspnœic arterial blood, partly owing to excitation of some centre for the uterine nerves existing in the cranium, and partly owing to irritation of excitable tissue in the uterus itself; and Schlesinger has further shown (Stricker's "Med. Jahrb.," 1873, p. 1) that uterine contractions can be induced by electric excitation of the centric extremity of a divided dorsal nerve. (For other experiments on the reflex contraction of the uterus after irritation of sensory nerves, see Spiegelberg, "Zeits. f. rat. Med.," 3 R. Band ii. 1858, Körner, "Studien des Phys. Inst. zu Breslau," Heft iii., and Obermeier, Pamphlet, Bonn, 1865.) Scanzoni found that irritation of the nipples, which, according to Luschka, contain so many tactile and Pacinian corpuscles, causes contraction of the uterus. The nerve plexus on the aorta is an important but not the only channel for the conduction of these motor impulses.

† Although nine calendar months, ten lunar months, forty weeks, or 280 days, is generally spoken of as the usual term of gestation, yet the real term exceeds this by from five to seven

this act, the muscular walls of the Uterus are primarily concerned; for a kind of peristaltic contraction takes place in them, the tendency of which is to press the contents of the cavity from the fundus towards the os uteri, and finally to expel them; and this contraction is alone sufficient to empty the uterus, when no impediment is presented to the exit of the fœtus, as we see in the occasional occurrence of *post-mortem* parturition. It is, in fact, in the contraction of the fibres of the fundus and body of the uterus, and in a relaxation of those about the cervix (which relaxation is something quite different from a mere yielding to pressure, and is obviously a vital phenomenon, that marks a peculiarity in the actions of this part), that the first stage of an ordinary labour essentially consists.* There is no proof whatever that these changes are dependent upon nervous influence; in fact, there is much evidence that the parturient action of the uterus is *not* the result (as some have maintained it to be) of a 'reflex' action of the Spinal Cord, but is due to its inherent contractility; for numerous instances have occurred in which normal parturition has taken place, notwithstanding the destruction of the lower part of the Cord, or the existence of a state of complete paraplegia which marked its functional inactivity; and the continuance of the peristaltic action for some time after somatic death, when neither the Cerebro-spinal nor the Sympathetic system can afford any supply of nervous power, is a yet more satisfactory proof of the same position.†—Nevertheless, it seems quite certain that muscular contractions of the Uterus *may be* induced by reflex action; for in no other way can we account for numerous phenomena, which distinctly mark the operation of remote causes acting through the nervous system; such as the induction of uterine contractions by the dash of cold water on the abdominal surface, by the injection of cold water into the vagina, by the ingestion of cold water into the stomach, or even by dipping the hand into cold water, or again by the suctorial application of the infant's lips to the nipple, by the introduction of the hand into the vagina, by violent movements of other parts of the body, by the presence of an excess of Carbonic acid in the blood, by anæmia produced by compression of the aorta, and by various other means. This general fact has an important practical bearing; since there are various occasions on which it is most important to life that the previously flaccid uterus should be excited to vigorous contraction, for the sake of accelerating parturition or of suppressing hæmorrhage; whilst, on the other hand, it is often no less important to be able to prevent or to antagonize the operation of causes which would prematurely induce uterine contractions, to the destruction of the offspring and the danger of the mother.

days, according to the months included. The mode of reckoning customary amongst women, is to date from the middle of the month after the last appearance of the catamenia: but it is certain that conception is much more likely to take place soon after they have ceased to flow, or even just before their access, than in the intervening period (§ 700), so that in the majority of cases it would be most correct to expect labour at forty weeks and a few days after the last recurrence of the menses. According to Dr. Matthews Duncan the interval between insemination and parturition is a period of 275 days. The interval between the disappearance of the last menses, and the period of parturition is considerably less than the usually assigned 280 days, and may be taken on the average to be 278 days. The real duration of pregnancy is, therefore, the period between conception and parturition, and this interval will be 275 days *minus* the interval between insemination and conception. Dr. Duncan, therefore, concludes that the 278th day after the last day of the last menses is the most *likely* one for parturition. The period of Quickening may be relied on in some women, in whom it occurs with great regularity in a certain week of pregnancy; but in general there is great latitude as to the time of its occurrence. The usual or average time seems to be about the 18th week of gestation.

* See a paper corroborating this statement, by Arthur Scott Dunkin, M.D., in "Edinb. Med. Journal," vol. ii. 1863, p. 523.

† See cases recorded in "Lancet," 1872, vol. i. pp. 517, 596.

720. When, in the normal act of Parturition, the head has so far made its way through the os uteri as to begin to distend the lower part of the genital canal, a new kind of expulsive effort is superadded to that of the Uterus itself; the assistance of the Expiratory muscles being then called in (§ 460), through the intermediation of the Spinal cord, which is probably excited to this action by the stimulus thus applied to the afferent nerves of the compressed parts; and it is chiefly by the instrumentality of these muscles that the normal act of parturition is usually completed. The same action which expels the fœtus, generally also detaches the placenta; and if the uterus contract with sufficient force after this has been thrown off, the orifices of the vessels which communicate with it are so effectually closed, that little or no hæmorrhage takes place. If, however, the uterus does not contract, or relaxes after having contracted, a large amount of blood may be lost in a short time from the open orifices. For some little time after parturition, a sero-sanguineous discharge, termed the *lochia*, is poured out from the uterus; and this commonly contains shreds of the deciduous membrane which had not been previously detached, together with a quantity of fat globules, and other products of disintegration of the uterine tissue.* Within a few weeks after delivery, the uterus regains (at least in a healthy subject) its previous condition; part of its newly-generated muscular fibres seem to disappear altogether, whilst the others shrink to their ordinary dimensions; and the portion of its mucous membrane which had been thrown-off as Decidua, seems to be to some extent reproduced. According to the researches of Dr. Matthews Duncan and M. Robin, this occurs even before delivery, so that the muscular tissue of the Uterus is never left completely denuded, though it does not become perfect until two months after delivery.†

721. As to the reason why the period of Parturition should be just forty weeks after the occurrence of Conception, we know nothing more than we do of that of similar *periodical* phenomena in the history of the life of Man and of other living beings; all of which must be considered as *occasional* manifestations of changes that are *constantly* in progress, whose rate, being dependent upon the degree of Heat supplied, is so uniform in warm-blooded amimals, as to secure a very close conformity to a common standard.‡ There is evidence that the occurrence of the uterine *nisus* may be induced by a variety of causes, several of which probably occur in the normal act of Parturition. For, in the first place, the state of development of the muscular substance of the Uterus can scarcely be without a considerable influence on this operation. We see it undergoing a gradual augmentation during the period of pregnancy, without any demand being made upon its functional activity; it gradually becomes more and more irritable, contractions being far more readily excited in it, by electrical or other stimulation, in the later than

* In addition to the evidence above referred to, of the rapid occurrence of fatty degeneration of the uterine structure after parturition, the Author may mention that he has been informed by Dr. Retzius (Professor of Midwifery at Stockholm) that he has detected a large number of fat-globules in the urine of puerperal women. Is it not possible—it may be further asked—that some of the oleaginous matter so copiously poured forth by the Mammary glands may be derived from this source? Such an economy of nutrient material would be consistent with what we elsewhere meet with; and the idea is conformable to the fact, that the proportion of butyrin in the milk is much greater in the earlier, than in the later months of lactation.

† See Huxley's "Elements of Comp. Anatomy," 1864, p. 107.

‡ This may be best illustrated by the analogy of a Leyden jar which is being charged by the *continuous* action of an Electrical Machine, and which is so arranged as to *dis*charge itself spontaneously whenever the disturbance in its equilibrium attains a certain intensity. If the movement of the machine be uniform, and other conditions remain the same, the discharge will take place at regular intervals.

in the earlier months of pregnancy; and at last this irritability seems to reach its acme, in virtue of the nutritive changes which have been progressively taking place in it, and to discharge itself in one powerful effort. Certain preparatory changes are known to be taking place in the Uterus itself, during the last two or three weeks of gestation; for its upper part contracts more closely around its contents, as if it were bracing itself up for the coming encounter; whilst there is a greater disposition to relaxation of its lower part, as also in the soft parts surrounding the orifice of the pelvis, so that the whole mass descends. It is well known that there is far less aptitude for dilatation in the os uteri before this change has taken place, so that premature labours are frequently rendered very difficult and tedious by the resistance which the fœtus encounters from the soft parts, notwithstanding that its smaller size enables it to pass more readily through the pelvic canal.—That the parturient effort, however, is not solely dependent upon the state of development of the uterus, appears from several considerations: and, in the first place, from the very curious fact that, in cases of extra-uterine fœtation, contractions resembling those of labour take place in its walls. In fact, what may be termed the *maturation* not merely of the Uterus, but also of its Embryonic contents—a condition analogous to that which precedes the dropping of ripe fruit, and which is acquired by the completion of the developmental process—appears to have more influence in determining the normal parturient effort, than any other cause which can be assigned. The Placenta of the fully-developed fœtus, indeed, is somewhat in the condition of the footstalk of a ripening fruit; that is, having attained its full evolution as an organ of temporary function, its connection tends to become dissevered in virtue of the further changes which take place in itself, quite irrespectively of any external agency.* This is very strikingly evinced by the fact, that when the uterus contains two fœtuses, and one of them is expelled—either in consequence of impeded development or disease in itself, or because it has attained its own full term of development (as in cases of superfœtation, § 724)—the other, if its development at this period is far from complete, is often retained, and goes on to its full term, *its* placenta not being detached in the first parturient effort, because it was not then prepared for the separation. It is obvious that this view affords a rational explanation of the occurrence of uterine action in cases of extra-uterine fœtation; for, if the condition of the placental attachment furnish its exciting cause, it will do so equally, whether the placenta be attached to the lining of the uterus, or to that of the Fallopian tube, or to any other organ. It is an additional indication that the immediate stimulus to the parturient effort of the uterus is given by some change in the condition of its fœtal connections, that the term of gestation seems capable of being prolonged by peculiarities in the constitution or rate of development of the fœtus, which are derived from the male parent; for it was ascertained by the late Earl Spencer,† that of 75 cows in calf by a particular bull, the average period was 288½ days, instead of 280; none of these having gone less than 281 days, and two-fifths of them having exceeded 289 days.

722. Various states of the constitution, especially that which is designated

* Such a change may be easily verified in the Placenta of many of the lower animals, such as that of the Cat, in which the fœtal and maternal portions remain more distinct from each other than they do in the Human female; for these become far more easily separable as the period of parturition draws near than they are at any previous time. De Sinéty ("Arch. de Physiol.," 1876, p. 342) states that it is impossible to ascribe the detachment of the placenta to the fatty degeneration of the decidua, for the quantity of fat they contain is in point of fact extremely minute.

† See Dr. J. C. Hall, in "Medical Gazette," May 6, 1842.

as 'irritability,' may induce the occurrence of the parturient effort at an earlier period; and this constitutes Premature Delivery or Abortion, according as the child is or is not *viable* (§ 723). There are some women in whom this regularly happens at a certain month, so that it seems to be an action natural to them; but it should always be prevented, if possible, being injurious alike to the mother and to the child; and this prevention is to be attempted by rest and tranquillity of mind and body, and by a careful avoidance of all the exciting causes which may produce uterine contractions by their operation on the Nervous system (§ 729). Among the causes of Abortion, however, the death of the fœtus, or an abnormal state of the placental structure, is one of the most common; and thus we have another very distinct proof of the influence which the state of the *contents* of the uterus has on the induction of the parturient effort.

723. The question of the *extreme limits* of the period of Gestation, is one of great importance both to the Practitioner and to the Medical Jurist.—In regard to the *shortest* period at which Gestation may terminate, consistently with the *viability* of the Child, there is still a great degree of uncertainty. Most practitioners are of opinion that it is next to impossible for a fœtus to live and grow to maturity, which has not nearly completed its seventh month; but it is unquestionable that infants born at a much earlier period have lived for some months, or even to adult age. It is rare in such cases, however, that the date of conception can be fixed with sufficient precision to enable a definite statement to be given. Of the importance of the question, a case which some time since occurred in Scotland affords sufficient proof. A vast amount of contradictory evidence was adduced on this trial; but, on the general rule of accepting positive in preference to negative testimony, it seems that we ought to consider it possible that a child may live for some months, which has been born at the conclusion of 24 weeks of gestation. In the case in question, the Presbytery decided in favour of the legitimacy of an infant born alive, within 25 weeks after marriage.* A like uncertainty exists

* "Report of Proceedings against the Rev. Fergus Jardine," Edinburgh, 1839. Several instances are on record of the survival of infants born at a very early period, thus:—A very interesting case is on record ("Edinb. Med. and Surg. Journal," vol. xi.) in which the mother (who had borne five children) was confident that her period of gestation was less than 19 weeks; the facts stated respecting the development of the child are necessarily very imperfect, as it was important to avoid exposing his body, in order that his temperature might be kept up; but three weeks after his birth he was only 13 inches in length, and his weight was no more than 29 oz. At that time, according to the calculation of the mother, he might be regarded as corresponding with an infant of 22 weeks or five months; but the length and weight were greater than is usual at that period, indicating that he was probably born at about the 25th week. It is an interesting feature in this case, that the calorific power of the infant was so low, that artificial heat was constantly needed to sustain it; but that under the influence of the heat of the fire he evidently became weaker, whilst the warmth of a person in bed rendered him lively and comparatively strong. During the first week it was extremely difficult to get him to swallow; and it was nearly a month before he could suck. At the time of the report he was four months old, and his health appeared very good.—Another case of very early viability has been more recently put on record by Mr. Dodd ("Provincial Medical and Surgical Journal," vol. ii. p. 474): in this, as in the former instance, the determination of the child's age rests chiefly on the opinion of the mother; but there appears no reason for suspecting any fallacy. The child seems to have been born at the 26th or 27th week of gestation, and having been placed under judicious management, it has thriven well.—One of the most satisfactory cases on record is that detailed by Dr. Outrepont, Professor of Obstetrics at Wurtzburg (Henke's "Zeitschrift," Band vi.), and stated by Dr. Christison in his evidence on the case first alluded to. The evidence is as complete as it is possible to be in any case of the kind; being derived not only from the date assigned by the mother to her conception, but also from the structure and history of the child. The gestation could have lasted only 27 weeks, and was very probably less. The length of the child was 13½ inches, and its weight was 24 oz. Its development was altogether slow; and at the age of eleven years the child

with regard to the degree of *protraction* of which the ordinary duration of Gestation is capable.—Many obstetric practitioners, whose experience should give much weight to their opinion, maintain that the regular period of 40 weeks is never extended by more than two or three days; whilst, on the other hand, there are numerous cases on record, which, if testimony is to be believed at all (and in many of these the character and circumstances of the parties place them above suspicion), furnish ample evidence, that Gestation may be prolonged for at least three weeks beyond the regular term.* In one case, indeed, recorded by Liegard,† pregnancy was believed to have lasted 330 days. The English law fixes no precise limit; and the decisions which have been given in our courts, when questions of this kind have been raised, have been mostly formed upon the collateral circumstances. The law of France provides that the legitimacy of a child born within 300 days after the death or departure of the husband shall not be questioned; and a child born after more than 300 days is not declared a bastard, but its legitimacy may be contested. By the Scotch law, a child is not declared a bastard, unless born after the tenth month from the death or departure of the husband.—Very important evidence on this subject is afforded by investigations on the lower animals, which are free from many sources of fallacy that attend human testimony. The observations of Tessier, which were continued during a period of forty years, with every precaution against inaccuracy, have furnished a body of results which seems quite decisive. In the Cow, the ordinary period of gestation is about the same as in the Human female; but out of 557 individuals, no less than 20 calved beyond the 298th day, and of these, some went on to the 321st, making an excess of nearly six weeks, or about *one-seventh* of the entire period. Of 447 Mares, whose natural period of gestation is about 335 days, 42 foaled between the 359th and 419th days, the greatest protraction being thus 84 days, or just *one-fourth* of the usual term. Of 912 Sheep, whose natural period is about 151 days, 96 yeaned beyond the 153rd day; and of these, 7 went on until the 157th day, making an excess of 6 days. Of 161 Rabbits, whose natural period is about 30 days, no fewer than 25 littered between the 32nd and the 35th; the greatest protraction was here *one-sixth* of the whole period, and the proportion in which there was a manifest prolongation was also nearly one-sixth of the total number of individuals. In the incubation of the common Hen, the duration of which must be entirely determined by the rate of embryonic development, Tessier found that there was not unfrequently a prolongation to the amount of three days, or *one-seventh* of the whole period.—In regard to Cows, the observations of Tessier have been confirmed by those of Earl Spencer, who has published‡ a table of the period of gestation as observed in

seemed no more advanced in body or mind than most other boys of seven years old. In this last point there is a very striking correspondence with the results of other observations upon premature children, made at an earlier age.—A very remarkable case has also been recorded by Dr. Barker, of Dumfries ("Medical Times," Sept. 7 and Oct. 12, 1850) in which the child is affirmed to have been born on the 158th day of gestation, or in the middle of the *twenty-third* week after intercourse. Its size, weight, and grade of development were conformable to the asserted period: for it weighed only 16 oz., and measured 11 inches; it had only rudimentary nails, and scarcely any hair except a little of reddish colour on the back of the head; the eyelids were closed, and did not open until the second day; the skin was shrivelled. When born it was wrapped up in a box and placed before the fire. The child did not suck properly until after the lapse of a month, and did not walk until she was nineteen months old. Three years and a half afterwards this child was in a thriving state, and very healthy but of small make; she then weighed 29½ lbs.

* A good collection of such cases will be found in Dr. Montgomery's excellent work on the "Signs of Pregnancy," and in Dr. A. Taylor's "Medical Jurisprudence."

† "Gaz. des Hôpitaux," 1859. ‡ "Journal of the English Agricultural Society," 1839.

764 individuals; he considers the average period to be 284 or 285 days; but no fewer than 310 calved after the 285th day; and of these, 3 went on to the 306th day, and 1 to the 313th. It is curious that among the calves born between the 290th and 300th days, there was a decided preponderance of males—these being 74, to 32 females; whilst all of those born after the 300th day were females. The additional series of observations subsequently made by Earl Spencer, in regard to the constant protraction of the period in 75 cows in calf by a particular bull, has been already noticed (§ 721).—Another series of observations has been published by Mr. C. N. Bement, of Albany, U.S.,* who has recorded the period of gestation of 62 cows. The longest period was 336 days; the shortest, 213 days. The average period for male calves was 288 days; and for females 282 days.—On the whole it may be considered, that in regard to the Human female, the French law is a very reasonable one; there being quite sufficent analogical evidence to support the assertions of females of good character, having no motive to deceive, which lead to the conclusion that a protraction of at least four weeks is quite possible, and that a protraction of six weeks is scarcely to be denied.†

724. There is another question regarding the function of the Female in the Reproductive act which is of great interest in a scientific point of view, and which may become of importance in Juridical inquiries—namely, the possibility of *Superfecundation*—that is, of two distinct conceptions at an interval of greater or less duration; so that two fœtuses of different ages, the offspring perhaps of different parents, may exist in the uterus at the same time. —The simplest case of Superfecundation is that in which a female has intercourse on the same day with two males of different complexions, and bears twins at the full time; the two infants resembling the two parents respectively. Thus, in the southern states of America, a black woman may bear at the same time a black and a mulatto child; the former being the offspring of her black husband, and the latter of her white paramour. The converse has occasionally, though less frequently occurred; a white woman having at the same time a white and a mulatto child. There is no difficulty in accounting for such facts, when it is remembered that nothing has occurred to prevent the uterus and the ovaria from being as ready for the second conception as for the first; since the decidua does not at first form a closed sac, as was formerly supposed, and consequently neither the orifice of the uterus nor of the Fallopian tubes is yet closed up; and, at the time when one ovum is matured for fecundation, there are usually more in nearly the same condition. Many such cases of alleged superfecundation are explicable upon the theory of atavism (§ 725).—But it is not easy thus to account for the birth of two children, which constitutes *Superfœtation*, each apparently mature, at an interval of five or six months; since it might have been supposed that the uterus was so completely occupied with the first ovum, as not to allow of the transmission of the seminal fluid necessary for the fecundation of the second. In cases where two children have been *produced* at the same time, one of which was fully formed, whilst the other was small and seemingly premature, there is no occasion whatever to imagine that the two were *conceived* at different periods; since the smaller fœtus may have been 'blighted,' and its development retarded, as not unfrequently happens in other cases. Nor is it

* "American Journal of the Medical Sciences," October, 1845.

† See especially two cases, 183 and 184, detailed by Dr. Murphy in his "Report of the Obstetric Practice of University College Hospital" for 1844; and another case published by him in the "Medical Gazette" for 1849, vol. xlviii. p. 683.

necessary to infer the occurrence of superfœtation in every case in which a living child has been produced a month or two after the birth of another; since the latter may have been somewhat premature, whilst the former has been carried to the full term. But such a difference can scarcely be, at the most, more than 2½ or 3 months;* and there are several cases now on record in which the interval was from 110 to 170 days, whilst neither of the children presented any indication of being otherwise than mature. In such cases, it is possible that there may have been a double uterus, the ova in the two portions of which may or may not have been impregnated on the same day.†

725. Whatever be the precise nature and history of the Fecundating process, there can be no doubt that the properties of the Germ depend upon conditions, both material and dynamical, supplied by *both* Parents. This is most obviously shown by the *fusion* of the characters of the parents, which is exhibited by *hybrids* between distinct species or strongly-marked varieties among the lower animals, such as the Horse and Ass, the Lion and Tiger, or the various breeds of Dogs; or in the offspring of parents belonging to two strongly-contrasted Races of Men, such as the European on the one hand, and the Negro or American Indian on the other.—It has long been a prevalent idea that certain parts of the organism of the offspring are derived from the male, and certain other parts from the female parent; and although no universal rule can be laid down upon this point, yet the independent observations which have been made by numerous practical 'breeders' of domestic animals (both mammals and birds), seem to establish that such a *tendency* has a real existence; the characters of the *Animal* portion of the fabric being especially (but not exclusively) derived from the *male* parent, and those of the *Organic* apparatus being in like manner derived from the *female* parent. The former will be chiefly manifested in the external appearance, in the general configuration of the head and limbs, in the organs of the senses (including the skin), and in the locomotive apparatus; whilst the latter show themselves in the size of the body (which is primarily determined by the development of the viscera contained in the trunk), and in the mode in which the vital functions are performed. Thus the *mule*, which is the produce of the male ass and the mare, is essentially a *modified ass*, having the general configuration of its sire (slightly varied by equine peculiarities), but having the rounder trunk and larger size of its dam; on the other hand, the *hinny*, which is the offspring of the stallion and the she-ass, is essentially a *modified horse*, having the general configuration of the horse (though with a slight admixture of asinine features), but being a much smaller animal than its sire, and thus approaching its dam in size, as well as in the comparative narrowness of its trunk. The influence of the female on the general 'constitution,' and especially on the fattening, milking, and breeding qualities of the offspring, is asserted to be proved by the history of several races of sheep and cattle, which have been most distinguished in these respects.§—But however *general* this rule may prove to be as regards

* For an interesting case of superfœtation, where the difference in the age of the two fœtuses was about three months, see a Report made by Drs. Harley and Tanner to the Obstetrical Society, "Lancet," vol. ii. 1862.

† See the Article 'Superfœtation,' in Dr. Beck's "Elements of Medical Jurisprudence," and R. B. Schultze in the "Jenaische Zeits.," Band ii. 1865, p. 1; and a Paper by Dr. Bonnar ("Edinburgh Med. Journal," Jan. 1865), for cases in which children succeeded each other very rapidly.

‡ For an excellent account of all the questions relating to Hybrids, reference may be made to Darwin's "Animals and Plants under Domestication."

§ See Walker 'On Intermarriage;' Orton on 'The Physiology of Breeding,' in the "Newcastle Chronicle," March 10, 1854; and Dr. Alex. Harvey 'On the Relative Influence of the Male and Female Parents in the Reproduction of the Animal Species,' in "Edinb. Monthly

the lower animals, it is by no means *universal;* for instances are by no means unfrequent, in which the multiple progeny of one conception divide between them the characters of the parents in very different modes. Thus, in a case in which a Setter-bitch, having been 'lined' by a Pointer, bore three pups, two of these pups seemed exclusively to resemble the father, appearing to be perfect Pointers in configuration, and growing-up with the habits of that race; whilst the third seemed equally to resemble its mother, being apparently a true Setter both in structure and instinct. Yet notwithstanding this apparent restriction, it subsequently appeared that the pointer-pups must have had something of the setter in their constitution, and the setter-pup something of the pointer. For one of the Pointer-pups (a male) having been matched at the proper age with a pointer-bitch of pure breed, one of the pups borne by the latter was a *true setter*, exactly resembling its paternal grandmother, and another was *setter-marked;* and the Setter-pup (a female) having been lined by a Setter-dog of pure breed, there were among its litter of pups two *pointers* resembling their maternal grandfather.—The same variety presents itself to even a greater degree in the human species. For in almost every large family (and sometimes even where there are no more than two children*), it will be observed that the likeness to the father predominates in some of the children, and the resemblance to the mother in others. Still it is rare to meet with instances in which *some* distinctive traits of *both* parents may not be traced in the offspring; these traits often showing themselves, in peculiarities of manner and gesture, in tendencies of thought or feeling, in proneness to particular constitutional disorders, &c., even where there is no personal resemblance, and where there has been no possibility that these peculiarities should have been gained by imitation. And even when they are overborne, as it were, in the immediate progeny, by the stronger influence derived from the other side, they will often reappear in a subsequent generation (as in the case just cited), constituting the phenomena known as *Atavism* or Reversion.†

726. The influence of both Parents on the constitution of the Offspring is strikingly manifested, not merely in the admixture of their characters normally displayed by the latter, but also in the tendency to *hereditary transmission* of perverted modes of functional activity which may have been habitual to either. The diseases which are usually considered to be most prone thus to reappear in successive generations are Scrofula, Gout, Syphilis, and Insanity; but it can scarcely be doubted that many others might be added to this list.‡ The predisposition may have been *congenital* on the part of the parents, or it may have been *acquired* by themselves, as in the case of Epilepsy transmitted by guinea-pigs in whom the sciatic nerve has been divided, to their young; and in no case is this more obvious than in the influence of Alcoholic excesses on the part of one or both parents, in producing Idiocy, a predisposition to Insanity, or weakness and instability of Mind, in the children,

Journ.," Aug. 1854; and especially Darwin "On the Variation of Species under Domestication," 1868.

* One of the most remarkable cases of this kind known to the Author, is that of two Sisters who seem to resemble each other in no one point of configuration or mental character; but of whom one bears a most striking resemblance, both in person and in mind, to her Father; whilst the other no less strikingly resembles her Mother. The only peculiarities which at all indicate their relationship, are a gouty diathesis which they both inherit from their father, and an idiosyncrasy in regard to opium, of which neither is able to take even a small dose (in any form whatever) without violent vomiting.

† Darwin, "Animals and Plants under Domestication," vol. ii. chap. xiii.

‡ See the very interesting and suggestive chapter 'On Hereditary Disease,' in Sir H. Holland's "Medical Notes and Reflections."

this being especially the case where both parents have transgressed. Thus, out of 359 Idiots, the condition of whose progenitors could be ascertained, it was found that no fewer than 99 were the children of absolute drunkards; and there was reason to believe that a large proportion of the parents of the remainder were more or less intemperate, only about a quarter of the whole number of idiots having been found to be the children of parents who were known to be temperate.* And it is perfectly well known to those who are conversant with Insanity, that, of all the 'predisposing causes' of that disorder, habits of intemperance on the part of either or both parents are among the most frequent.—The intensification which almost any kind of perversion of Nutrition derives from being common to *both* parents, is most remarkably evinced by the lamentable results which too frequently accrue from the marriage of individuals nearly related to each other and partaking of the same 'taint.' Such results must have fallen within the knowledge of almost every one possessing an extended field of observation; but they are brought out with fearful vividness by the unerring test of properly collected Statistics. For out of the 359 idiots just referred to, 17 were *known* to have been the children of parents nearly related by blood; and this relationship was *suspected* to have existed in several other cases in which positive information could not be obtained. On examining into the history of the 17 families to which these individuals belonged, it was found that they had consisted, in all, of 95 children; that of these no fewer than 44 were idiotic, 12 others were scrofulous and puny, 1 was deaf, and 1 was a dwarf. In some of these families all the children were either idiotic or very scrofulous and puny; in one family of 8 children, 5 were idiotic.†—But it does not seem requisite for the production of very imperfect offspring from the intermarriage of near relations, that any decided 'taint' should exist in the parents; for the Author's own observations and inquiries lead him to conclude that the same danger results when there is any strong personal or mental 'idiosyncrasy,' such as is often seen to run through the members (both male and female) of a particular family, causing them to be at once recognized as belonging to it,

* See Dr. Howe's "Report on Idiocy to the Legislature of Massachusetts," 1848.

† See Dr. Howe's Report, p. 90. An Abstract of this Report is given in the "Amer. Journ. of Med. Sci.," April, 1849.—The following works may also be referred to as containing information upon the important subject of the effects upon the offspring of marriages of consanguinity:—M. Boudin in the "Annales d'Hygiène," vol. xviii. pp. 6–82, who observes that the deaf-mutes of consanguineous origin are from twelve to fifteen times as numerous as they would be if the infirmity were equally distributed among the offspring of consanguineous and other marriages; Dr. Bemiss in the "Journal of Psychological Medicine" for 1857, p. 368, who supplies facts and arguments against such marriages; Dr. Mitchell in the "Edinb. Med. Journ." for 1862, p. 872, who considers idiocy to be an especially frequent consequence of the marriage of blood-relations, and agrees with M. Boudin in regard to the frequency of deaf-mutism in the offspring; M. Cadiot in the "Comptes Rendus," vol. ii. 1863, p. 978; M. Angelon in idem, vol. i. 1864, p. 166; and Dr. E. Dally in the "Anthropological Review" for May, 1864. See also "Essays on Physiological Subjects," by G. W. Child, pp. 1–55, 1869; Herbert Spencer's "Principles of Biology," vol. i. pp. 281–283, and Dr. Galton "On the Influence of Heredity." Amongst the Editor's own immediate relations there have been five marriages between first cousins, from which have proceeded thirty-three children; of these, eight have died, one from teething, two from croup, and one from hooping-cough (all injudiciously fed), one from accident, one from cyanosis, and two from well-marked scrofulous disease; the last two occurred in the same family, and were the only offspring of an extremely obese father and a highly scrofulous mother. The surviving children are of unusually healthy and fine growth. See also a Leader in "Lancet," 1870, vol. ii. p. 898. The Editor, therefore, from these and other observations, fully accords with the observations of Dr. G. W. Child in the "Medico-Chir. Review" for 1862, vol. i. p. 461, who, in criticizing Dr. Bemiss's Essay, remarks that the marriages of blood-relations have no tendency, *per se*, to produce degeneration of race, though they have a tendency to strengthen and develop in the offspring individual peculiarities of the parents, both mental and physical, whether morbid or otherwise.

by those who have been familiar with other members.* Dr. Darwin† has also shown that long continued and close interbreeding between the nearest relations diminishes the constitutional vigour, size, and fertility of the offspring; and occasionally leads to malformations, but not necessarily to general deterioration of form and structure. This liability probably does not exist to nearly the same degree, where the parents, although nearly related, differ widely in physical and in psychical characters, through the predominance of elements which have been introduced by *their* non-related parents; as, for example, when a man strongly resembles his *father* rather than his mother, marries the daughter of his *mother's* brother, who, on her part, resembles her own *mother* rather than her father. But the case previously cited (§ 725) gives warning that even here the 'family idiosyncrasy' may exist in a powerful degree, though in a latent form, and may seriously affect the constitution of the offspring. It is quite as common to meet with Atavism in the transmission of hereditary disease as in the reproduction of 'family likeness.'

727. Attention has also been directed to a very curious class of phenomena, which show that where the mother has previously borne offspring, the influence of *its* father may be impressed on her progeny afterwards begotten by a different parent: as in the well-known case of the transmission of Quagga-marks to a succession of colts, both of whose parents were of the species Horse, the mare having been once impregnated by a Quagga male;‡ and in the not unfrequent occurrence of a similar phenomenon in the Human species, as when a widow who marries a second time bears children strongly resembling her first husband. Some of these cases appear referable to the strong mental impression left by the first male parent upon the female; but there are others which seem to render it more likely that the blood of the female has imbibed from that of the fœtus, through the placental circulation, some of the attributes which the latter has derived from its male parent; and that the female may communicate these, with those proper to herself, to the subsequent offspring of a different male parentage.§—This idea is borne out by a great number of important facts; and it serves to explain the circumstance well known to practitioners, that secondary syphilis will often appear in a female during gestation or after parturition, who has never had primary symptoms, whilst the father of the child shows no recent syphilitic disorder. For if *he* have communicated a syphilitic taint to the fœtus, the mother may become inoculated with it through her offspring in the manner just described. As this is a point of great practical importance, it may be hoped that those who have the opportunity of bringing observation to bear upon it will not omit to do so.

728. There seems good reason to believe, moreover, that the attributes of the Germ are in great degree dependent, not merely upon the *habitual* conditions of the Parents which have furnished its original components, but even upon the condition in which those parents may be at the time of sexual congress. Of this we have a remarkable proof in the phenomenon well known to

* A most lamentable instance of this kind, which happened some years ago in a family well known to the Author, was the occasion of his first directing his attention specially to this point. Two first-cousins, possessing a strong 'family idiosyncrasy,' but no definite 'taint,' having married, four children were born, each of which was distinguished by some marked effect of organization or perversion of function, one being deaf and dumb, another scrofulous, a third idiotic, and a fourth epileptic.

† Op. cit. vol. ii. p. 159, ed. Murray, 1875. ‡ "Philosophical Transactions," 1832.

§ See an interesting discussion of this question, by Dr. Alex. Harvey, in the "Edinb. Monthly Journ.," Oct. 1849, and Oct. and Nov. 1850; and in his pamphlet "On a Remarkable Effect of Cross-breeding," Edinb. 1851.

breeders of animals, that a strong mental impression made upon the female by a particular male, will give the offspring a resemblance to him, even though she has had no sexual intercourse with him;* a circumstance for which there is no difficulty in accounting, on the hypothesis already put forth regarding the dynamical relation of mental states to the Organic processes (Chap. XVII.). On the whole, then, we seem entitled to conclude, that the attributes of the embryo will be influenced in a most important degree by the entire condition (as relates both to the organic and the psychical life) of both parents at the time of the sexual congress; and it is probably on account of the perpetual changes taking place in the bodily and mental state of each individual (his condition at any one time being the general resultant of all those changes), that we almost constantly witness marked differences between children born at successive intervals, however strong may be the 'family likeness' among them; whilst the resemblance between twins is almost invariably much closer.†

729. When it is borne in mind that, during the entire period of gestation, the Embryo is deriving its nutriment exclusively from the blood of the Mother, and that the condition of this fluid in relation to her own processes of Nutrition and Secretion, is subject to a very marked influence from her own mental states (Chap. XVII.), it cannot fairly be thought improbable, that the developmental processes of the Embryo should be powerfully affected by strong Emotional excitement on her part. Among the facts of this class, there is, perhaps, none more striking than that quoted by Dr. A. Combe‡ from Baron Percy, as having occurred after the siege of Landau in 1793. In addition to a violent cannonading, which kept the women for some time in a constant state of alarm, the arsenal blew up with a terrific explosion which few could hear with unshaken nerves. Out of ninety-two children born in that district within a few months afterwards, Baron Percy states that 16 died at the instant of birth; 33 languished for from eight to ten months, and then died; 8 became idiotic, and died before the age of five years; and 2 came into the world with numerous fractures of the bones of the limbs, probably caused by irregular uterine contractions. Here, then, is a total of 59 children out of 92, or within a trifle of 2 out of every 3, actually killed through the medium of the Mother's alarm, and the natural consequences upon her own organization; an experiment (for such it is to the Physiologist) upon too large a scale for its results to be set down as mere 'coincidences.'—No soundly-judging Physiologist of the present day is likely to fall into the popular error of supposing that 'marks' upon the Infant are to be referred to some *transient* though strong impression upon the imagination of the Mother; but there appear to be a sufficient number of facts on record to prove that *habitual* mental conditions on the part of the Mother *may* have influence enough, at an early period of gestation, to produce evident bodily deformity, or peculiar tendencies of the mind. The error of the vulgar notion on this subject lies in supposing that *a sudden fright, speedily forgotten*, can exert such a continual influence on the nutrition of the Embryo, as to occasion any personal peculiarity.§ The view here stated is one which ought to have great

* See Harvey, loc. cit.

† Where twins are very unlike one another, it will usually be found that the dissimilarity is due to the predominance of the characters of the father in one, and of those of the mother in the other; as in the case of the Pointer and Setter previously cited (§ 725).

‡ "On the Management of Infancy," p. 76.

§ For some valuable observations on this subject, see Montgomery "On the Signs of Pregnancy."—Numerous cases were recorded a few years since (especially in the "Lancet" and "Provincial Medical Journal") in which malformations in the Infant appeared distinctly

weight, in making manifest the importance of careful management of the health of the Mother, both corporeal and mental, during the period of pregnancy; since the ultimate constitution of the offspring so much depends upon the influences then operating upon its most impressible structure.

4. *Development of the Embryo.**

730. The history of the evolution of the Germ, from its first appearance as *a single cell* lying in the midst of the yolk, to the time when it presents the form and structure characteristic of its parent species, and is capable of maintaining an independent existence—including the details of the progressive development of each separate organ, from its first appearance as an aggregation of simple cells formed by the duplicative subdivision of the primordial vesicle, to that stage of completeness in which it is able to bear a part in the vital economy of the new being—and embracing, also, the succession of changes in the provisions for the nutrition of the embryo in the successive phases of its existence, and the adaptations of its general organization to each respectively—constitutes one of the most interesting departments of Physiological Science, and one which has of late years received a peculiar degree of attention. It is a branch of the inquiry, however, which has, and seems likely to have, less *practical* bearing than any other; for neither as regards the preservation of the body in health, nor its restoration from disease, is it easy to see what direct benefit the most exact knowledge of Embryonic Development is likely to afford. The chief subject on which it throws light, is that of Congenital Malformations and Deficiencies; many of which are now distinctly traceable to *arrest* or *irregularity* of the developmental processes; some of them, indeed, to *excess*. For these reasons, the topic before us will be passed over much more lightly in the present Treatise, than its scientific importance might seem to demand; and all that will be here attempted, will be a mere sketch of the mode in which the evolution of the germ takes place, this being followed in the first instance as a whole, whilst its principal organs will be afterwards separately considered as they successively present themselves.—This sketch, however, will serve to convey an idea of the nature of the process, and to illustrate its conformity in Man to that great law of progress *from the general to the special*, which is equally manifested in the development of every other organized being.

731. When we first discern the primordial cell which is to evolve itself into the Animal organism, we can trace nothing that essentially distinguishes it from that which might give origin to *any* other form of organic structure; its condition, in fact, being alike in all, and permanently represented by the humblest single-celled Plants and Animals. The earliest stage of its development consists in simple multiplication by 'duplicative subdivision' of its contents, so that a mass of cell-like bodies comes to be produced, amidst the several components of which no difference can be traced; and this also finds its parallel among the simpler organisms of both kingdoms. Soon, however, this *homogeneous* condition gives rise to a *heterogeneous* one; the further

traceable to strong impressions made on the mind of the Mother some months previously to parturition; these impressions having been persistent during the remaining period of pregnancy, and giving rise to a full expectation on the part of the Mother that the child would be affected in the particular manner which actually occurred. Of one very striking case of this kind the Author is personally cognizant, it having occurred in a family of a near connexion of his own.

* The Anatomy of the Human Embryo may be studied in the work of Wilhelm His, which is at present being issued by Vogel of Leipzig, 1880.

changes which different parts of this mass undergo, not being of the same uniform character, so that a marking out of *organs*, or instrumental parts adapted for different purposes in the economy, begins to be discernible. A marked divergence, as was shown by Reichert, occurs, however, at a very early period, according to whether the whole contents of the ovum undergo segmentation, and are directly converted into the growing embryo, or whether only a portion is thus segmented, the remainder forming a bag over which vessels are developed, effecting the absorption of its contents, and thus enabling it indirectly to participate in the process of development. The former kind of egg, consists, therefore, altogether of germ yolk; the latter of a small germ yolk,* and a large food yolk.† Ova in which the former arrangement holds are termed *holoblastic*, and are represented by Mammals generally, Batrachia, Cyclostomata, and Amphioxus amongst the Vertebrata, and by the simpler forms of Crustacea and Arachnida, the Annelida, lower Mollusca, Entozoa, and Echinodermata amongst the Invertebrata. The ova in which the latter arrangement holds, are termed *meroblastic*, and are represented by Birds, Reptiles, Fish, with the exception of the Cyclostomes amongst the Vertebrata, and by the Cephalopoda, and higher orders of Crustacea and Arachnida amongst the Invertebrata. In the fowl, according to His (loc. cit. p. 39), the whole of the nervous system, the whole of the muscular system (both striated and unstriated), the true epithelial structures and the glands proceed from the development of the morphological elements of the cicatricula, whilst the blood and the connective tissues, together with the endothelial lining of the blood-vessels, proceed from the so-called white yolk. The organs whose distinctness first becomes apparent, are not (for the most part) those which we trace in the completed structure, but have a merely temporary character; being evolved either as a sort of scaffolding or frame-work for the building up of the more permanent parts, or with a view to the nutrition of the embryo during the evolution of these. Although the first indications of heterogeneousness in the general mass are of nearly the same kind in all animals—consisting in the formation of a *blastodermic membrane* (composed, however, of nothing else than layers of cells) upon its exterior, which serves as a sort of temporary stomach, whilst a large part of the included mass undergoes liquefaction, and serves as the nutrient material for the tissues which are to be evolved from it—yet indications are very speedily manifested, of the *primary division* of the Animal Kingdom of which the new being is a member. In the case of the Human embryo, as in that of all Vertebrate animals, the first outline of the permanent organization is shown in the 'primitive trace,' which fades away, and above which appears the medullary groove, marking out the line of the vertebral column (Plate II., Fig. 11); and in this we very soon discern the foundations of the separate vertebræ (Fig. 333, *pr*). But there is nothing at this period to distinguish the germ of Man from that of *any other* Vertebrate animal, this early part of the developmental process being carried on upon the same plan in every member of that sub-kingdom; and it is not until we meet with indications of one of the plans which are peculiar to the respective classes of that sub-kingdom, that we can discover whether the germ in course of evolution is to become a Mammal, Bird, Reptile, or Fish. So, even when it has been recognized as belonging to the Mammalian class, there is at first nothing to distinguish it from that of any other Mammal; and it is only with the advance of the developmental process that indications successively present themselves, which enable us to distinguish, one after another, the characters

* The *Protoplasm* of Van Beneden. † The *Deutoplasm* of the same author.

of the order, the family, the genus, the species, the variety, the sex, and the individual—*the more special features progressively evolving themselves out of the more general*, which is the expression of the law of development common to all Organized beings.

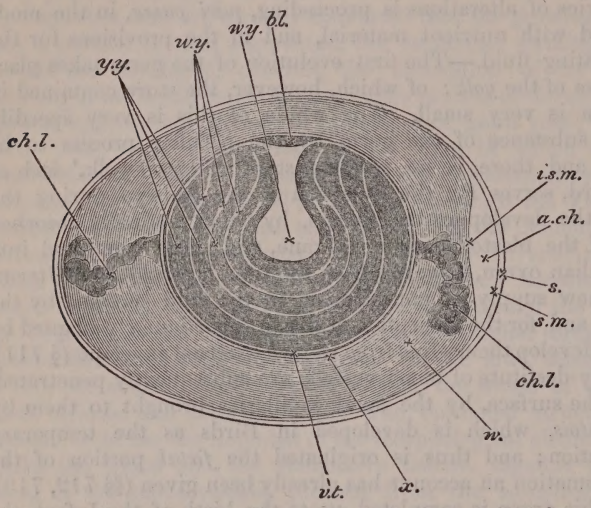
732. With this progressive alteration in the condition of the embryo itself, a very remarkable series of alterations is proceeding, *pari passu*, in the mode in which it is supplied with nutrient material, and in the provisions for the aëration of its circulating fluid.—The first evolution of the germ takes place entirely at the expense of the *yolk:* of which, however, the store contained in the Mammalian ovum is very small. The whole of this is very speedily incorporated in the substance of the germ, by the peculiar process to be presently described; and there is no residual store of 'food-yolk,' such as that which, in the Bird, serves for the nutrition of the embryo during the whole remainder of the developmental process, by being gradually absorbed into the substance of the blastodermic membrane, and there converted into blood. The Mammalian ovum, however, from the time it reaches the Uterus, is furnished with a new supply of nourishment, in the fluid secreted by the Decidual membrane; and, for the absorption of this, it is particularly adapted by the villosities which develop themselves from its own external envelope (§ 711). These, at first entirely destitute of blood-vessels, are subsequently penetrated, at a certain part of the surface, by the fœtal capillaries brought to them by an organ, the *Allantois*, which is developed in Birds as the temporary instrument of respiration; and thus is originated the *fœtal* portion of the Placenta, of whose formation an account has already been given (§§ 712, 713). From the time that this organ is completed, up to the birth of the Infant, the embryo draws its nutrient materials direct from the maternal blood, though not receiving that blood *as such* into its own organism, since there is no direct communication between the blood of the fœtus and that of the mother; and it is through the same medium that the aëration of its own blood is effected, its pulmonary apparatus being as yet inoperative. Its circulating system, arranged in accordance with these requirements, presents many peculiarities which mark its fœtal character; and the alteration in the course of the blood, which takes place as soon as the respiratory organs come into play, constitutes the essential difference between intra-uterine and extra-uterine life. If, as sometimes happens, the lungs of the new-born infant expand but imperfectly or scarcely at all, the circulation continues to be carried on in a greater or less degree upon its intra-uterine plan; and this, when the placenta is no longer capable of supplying the needed aëration, is incompatible with the persistence of life.

733. The early stages of the development of the Embryo in Vertebrata are much better known in the Bird than in the Mammal, on account of the facilities which the eggs of these animals offer for examination, and it will be expedient, therefore, to describe the course of events in them: noting the principal differences that have been observed in the process as it occurs in the higher class.* A newly-laid hen's egg consists of a shell (Fig. 326, *s*),

* In the following account, Foster and Balfour's "Elements of Embryology" has been taken as a guide, and to this excellent work the student is referred for details that considerations of space preclude from being here inserted; but other works and researches which may be studied are those of Rathke, "On the Development of the Snake," 1839, and of the Tortoise, 1848,—of Kölliker (Müller's "Archiv," 1843, p. 68) and Bagge ("De Evolut. Strongyli et Ascarid., Diss. Inaug.," 1841) on the ova of *Entozoa*,—Kölliker's "Entwickelungsgeschichte des Menschens," 1879,—those of v. Baer, "On the Development of the Fish," 1835,—those of Newport ("Philos. Transact.," 1851) and Dugès ("Récherches sur les Batraciens," 1835) on the ova of *Batrachia*,—those of Bischoff ("Entwickelungsgeschichte des Hundes-

composed of an organic basis impregnated with calcic salts, and perforated by vertical canals, through which an interchange of gases can take place. The shell is lined by two layers of membrane (Fig. 326, *s m*, *i s m*), which early separate from each other at the broad end to form the air-chamber. Beneath the shell membrane is the white of the egg, or albumen (Fig. 326, *w*); and stretching from near the two extremities of the egg to the opposite surfaces of the yolk, are two twisted portions of rather firmer albumen, termed the *chalazæ* (*ch*, *l*), which perhaps serve to keep the yolk in position. The yolk is enclosed in the *vitelline membrane* (*vt*), and by far the largest portion of it is composed of *yellow yolk* (*yy*), which consists of spheres, never containing a nucleus, but filled with minute, highly refractile granules. The yellow yolk is surrounded by a thin layer of a lighter-coloured yolk, the *white yolk* (*wy*), which dipping into it at one point, forms a flask-shaped mass in its interior. The white yolk also forms a series of concentric layers (*halones*) in the substance of the yellow yolk. It is composed of spherules, for the most part smaller than those of the yellow yolk, with a highly refractive nucleus-like body in the interior of each, and of larger spheres, each of which contains a number of spherules similar to the smaller spherules; it presents also some

FIG. 326



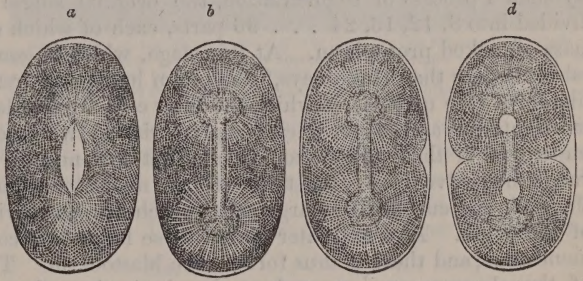
Diagrammatic Section of an Unincubated Fowl's Egg. *bl*, blastoderm; *w*, *y*, white yolk. This consists of a central flask-shaped mass and a number of layers—the halones—concentrically arranged around this; *y*, *y*, yellow yolk; *v*, *t*, vitelline membrane; *x*, layer of more fluid albumen immediately surrounding the yolk; *w*, albumen, consisting of alternate denser and more fluid layers; *ch*, *l*, chalaza; *a*, *ch*, air-chamber at the broad end of the egg. This chamber is merely a space left between the two layers of the shell-membrane; *i*, *s*, *m*, internal layer of shell membrane; *s*, *m*, external layer of shell membrane; *s*, shell.

eies," 1845) on the ova of the *Bitch*,—those of Remak on the Vertebrata ("Untersuch. über die Entwickel. der Wirbelthiere," Berlin, 1855)—of Reichert on the Guinea-pig ("Beiträge zur Entwickelungsgeschichte des Meerschweinchens"), "Monatsbericht d. Akad. Berlin," 1860—of Leuckart contained in Wagner's "Handwörterbuch der Physiologie," art. 'Zeugung,'—of Allen Thomson in the art. 'Ovum,' in the supplementary volume to Todd's "Cyclop. of Anatomy and Physiology," 1859, Quain's "Anatomy," vol. ii. ed. 8, 1878, and 'Address, before British Assoc.' 1877, "Nature," vol. xvi. p. 302,—of Huxley in the Croonian Lecture for 1858, and in his "Lectures on the Elements of Comparative Anatomy," 1864,—of Coste ("Histoire Génér. et Partic. du Développement des Corps Organisés," 1847–1859),—of Pander, "Beiträge zur Entwick. d. Hühnchens,"—of His, "Untersuchungen über die erste Anlage des Wirbelthierleibes," Leipzig, 1868,—of v. Beneden, "Récherches sur la composition et la signification de l'Œuf," 1870,—of Oellacher, Schultze's "Archiv f. mic. Anat.," Band viii. 1872; Goette "On the Development of the Bombinator igneus," 1875, and of Parker's various papers 'On the Development of the Skull,' in "Philosophical Transactions;" Balfour, "On the Development of the Elasmobranch Fishes," 1878, and Humphry and Turner's "Journal of Anat. and Physiol." vols. x.–xii.; 'Some Teachings of Development,' "Quarterly Journal of Microscop. Sci." 1880; Schäfer 'On the Early Stages of Development in the Cat's Ovum,' "Proc. Roy. Soc." 1876; 'The Development of the Guinea-pig,' Humphry and Turner's "Journal of Anat. and Physiol.," vol. x. p. 771; vol. xi. p. 332.

vacuoles in the region of the cicatricula. At the point where the white yolk dips into the yellow yolk is a depression, which is occupied by a small white disk, about the sixth of an inch in diameter, termed the *blastoderm* or *cicatricula* (*bl*). The disk is always uppermost when the egg is opened from the side, in consequence of the lighter specific gravity of this part of the vitellus. A typical cicatricula presents an outer white rim, or *area opaca*, a circular transparent area, or *area pellucida*, and a more or less well-marked central opacity. The area opaca and central opacity appear to be due to the disposition of the white yolk beneath the blastoderm, whilst in the part corresponding to the area pellucida, the blastoderm is separated from the white yolk by a space, filled with a little fluid. Imbedded in the protoplasm of the germinal disk is a globular or ellipsoidal highly refractile body, termed the *germinal vesicle;* in the interior of which, again, is a small body, the *germinal spot.*

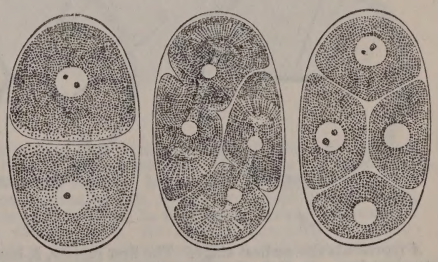
734. The ovum of the Mammal differs from that of the bird in not presenting the same differentiation into white and yellow yolk and cicatricula, but resembles the cicatricula in undergoing complete cleavage or segmentation. The ovum is therefore said to belong to the holoblastic type. It is originally composed of yolk spheres diffused in protoplasm, and contains a germinal vesicle and germinal spot. The process of segmentation in the Mammalian and other ova has recently been studied with great care by several observers, notably by Auerbach,* Bütschli,† Strasburger,‡ Van Beneden, Hertwig, Priestley, and Balfour;§ and the results which have been attained are thus summed up by Mr. Priestley: The primary segmentation nucleus, whose previous history has been already traced (§ 707), elongates so that a spindle-shaped body (Fig. 327) is produced. The extremities of the nucleus exhibit clearer spaces, which radiate into the granular protoplasm, and are united with each other by clear lines, one on each side of the body of the nucleus. During this process the body of the nucleus has become

FIG. 327.



Ovum of Ascaris nigrovenosa, showing the method formation of the bistellate figure, and segmentation into two.

FIG. 328.



Ovum of Ascaris nigrovenosa, showing segmentation into four. In the course of the elongation and formation of the bistellate figure, the positions of the segments change from superior and inferior to supra-lateral and infero-lateral.

* "Organologische Studien," Breslau, 1873–4.

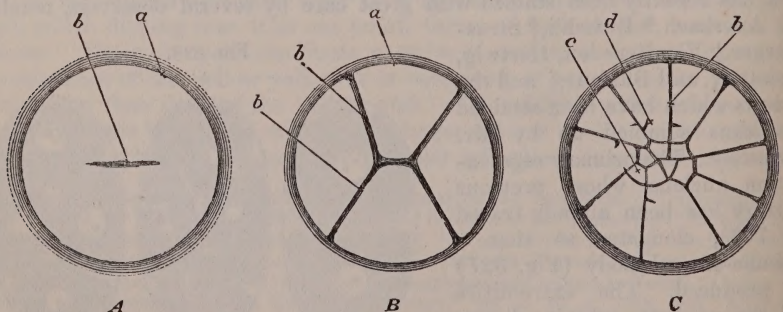
† "Nov. Act. Nat. Cur." 1873; and "Zeitsch. f. wiss. Zool.," vol. xxv.

‡ "Ueber Zellbildung und Zelltheilung," Jena, 1875.

§ "Quart. Journ. Mic. Sci.," vol. xvi. p. 137. For an account of the results obtained by these observers, see a Paper by Mr. Priestley in "Quarterly Journal of Microscopical Science," vol. xvi. (1876) pp. 131, 153.

smaller, and it finally disappears, leaving two 'asters' with an intermediate band (Fig. 327 *d*). The granules of the cell substance now begin to recede from a portion of the wall, and a lateral inversion of the margin occurs. The portion thus invaginated is rapidly converted into a furrow, extending around the circumference of the ovum, but beneath the vitelline membrane which is not involved in the process. The furrow deepens, and the protoplasmic mass is thus constricted till it forms two distinct portions (Fig. 328 *a*). Whilst the furrow is still shallow, two vacuoles appear in the band uniting the stars on each side of, and close to, the plane of the equator; these vacuoles commence a movement towards the centres of their respective halves. In the mean time the stellate figures in each half shrink, and as they do so the newly-formed vacuoles increase in size (Fig. 328 *a*). On reaching their destinations the nuclei acquire nucleoli, the bistellate figures gradually disappear, and the division of the ovum into two is complete (Fig. 328 *a*). The subsequent stages of cleavage (Fig. 328 *b*) are but a repetition of the steps above described, except that the later divisions do not appear to involve the entire ovum, as do the first four or five. By such a process of segmentation, the original single ovum becomes subdivided into 8, 12, 16, 24 . . . 96 parts, each of which consists of a nucleated mass of naked protoplasm. At this stage, which is generally reached in the rabbit in less than three days,* the ovum having at first assumed a mulberry-like form (the morula), in which the outer cells are smaller and project over the more internal and larger ones, has given rise to two layers of cells. The more superficial of these cells become somewhat flattened by mutual pressure, and range themselves closely together to form a nucleated cellular layer, which covers the yolk and encloses the large cells, which are also divided from the cleavage of the ovum. At a still later period these large cells cohere to form a second membrane, and there is thus formed the blastoderm. This constitutes the end of the cleavage process, and at the time when the ovum passes into the uterus, the embryo is composed of these two layers, the one being the

FIG. 329.



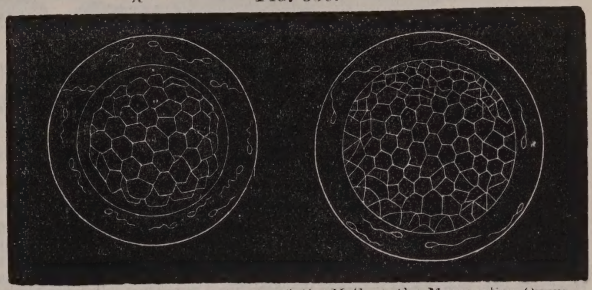
A represents the earliest stage. The first furrow, *b*, has begun to make its appearance in the centre of the germinal disk. In *B* the first furrow is completed right across the disk, and a second similar furrow nearly at right angles to it has appeared. The disk thus becomes divided somewhat irregularly into quadrants by four (half) furrows. In a later stage (*C*) the meridian furrows (*b*) have increased in number from four, as in *B*, to nine, and cross furrows have also made their appearance. The disk is thus cut up into small central (*c*) and larger peripheral (*d*) segments. Several new cross furrows are seen just beginning, as, ex. gr., close to the end of the line of reference (*d*).

ectoderm, the other the mass of endoderm. In birds, the process of cleavage is somewhat different, although it is probably the same in principle. The egg is meroblastic—that is to say, it undergoes only partial segmentation, which is restricted to the cicatricula or germinal disk. The cleavage occurs during the

* Allen Thompson, 'British Assoc. Address, 1877,' "Nature," vol. xvi. p. 307.

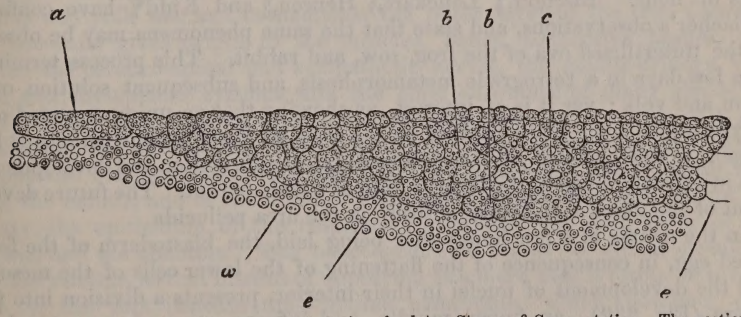
passage of the egg through the oviduct, a progress which usually occupies about twenty-four hours in the common fowl. During this passage the ovum receives the coating of albumin, which afterwards forms the white of the egg, and at the lower part of the oviduct the investing membrane and the shell. The segmentation commences with the formation of a furrow, which is quickly crossed by another at right angles, and soon by others. The examination of hardened specimens of the bird's egg shows that the segmentation is not confined to the surface, but extends through the mass of the blastoderm, and that it takes place not only by vertical but by horizontal furrows, that is, by furrows parallel to the surface of the disk. The original germinal disk is thus broken up, as in the Mammal, into a number of small masses of protoplasm, which are smallest in the centre of the disk and upon the surface; the smaller size of the superficial layer foreshadowing the subsequent division of the blastoderm into two layers, which form the true blastoderm,* or germinal membrane of Pander (Fig. 331). The disk having undergone segmentation

A FIG. 330. B



Later stage in the *Segmentation of the Yolk* of the Mammalian Ovum:—at A is shown the 'mulberry-mass' formed by the minute subdivision of the vitelline spheres; at B, a further increase has brought its surface into contact with the vitelline membrane, against which the spherules are flattened.

FIG. 331.



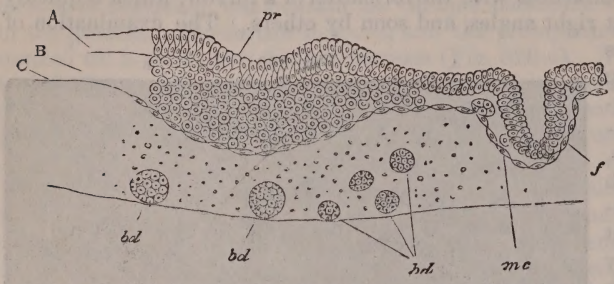
Section of the Germinal Disk of a Fowl during the later Stages of Segmentation. The section, which represents rather more than half the breadth of the blastoderm (the middle line being at *c*), shows that the upper and central parts of the disk segment faster than those below, and at the periphery. In the majority of segments a nucleus can be seen, and one is probably present in all. The segments contain a number of highly refracting spherules. In the central part of the blastoderm the upper cells have commenced to form a distinct layer. No segmentation cavity is present. *a*, large peripheral cell; *b*, larger cells of the lower parts of the blastoderm; *c*, middle line of blastoderm; *e*, edge of the blastoderm adjoining the white yolk; *w*, white yolk.

becomes separated from the white yolk, on which it has hitherto been lying, by a space containing fluid, termed the *segmentation cavity* (see Fig. 332), and with this a distinction becomes apparent between the upper and lower layers of

* For theories in regard to the formation of the blastoderm by secondary segmentation see Ray Lankester 'On the Ova of Cephalopoda,' "Ann. and Mag. of Nat. Hist.," 1873, p. 31; Balfour, 'Development and Growth of the Layers of the Blastoderm,' "Quarterly Journal Microscop. Sci.," 1873, 1874 and 1880; Goette, "Archiv f. Mikroskop. Anat.," x. 1874, and Van Beneden, 'La formation des feuillets chez le Lapin,' "Archiv de Biologie" (1880), tom. i. pp. 128–220.

the segmentation masses. Those of the upper or superficial series assuming a columnar form, and presenting well-defined nuclei, arrange themselves side by side, and constitute a kind of membrane, the Ectoderm or Epiblast (Fig. 331 *a*); whilst those on the lower series, which form the Endoderm, in turn give rise to the Mesoblast and Hypoblast, remain larger (*b*), have no nucleus, or only an indistinct one, and form rather a close irregular network than a distinct membrane. A few of the cells of this layer, constituting the so-called *formative cells** (*bd*, Fig. 332) becoming detached, fall to the bottom of the segmentation cavity, and rest on the white yolk. This is the usual condition of the blastoderm at the time that the egg is laid. Œllacher† describes a process of cleavage similar to that above described, which he has observed in the unimpregnated eggs of hens. Bischoff,‡ Leuckart,§ Hensen,‖ and Kidd¶ have confirmed Œllacher's observations, and state that the same phenomena may be observed in the unfertilized ova of the frog, sow, and rabbit. This process terminates in a few days in a retrograde metamorphosis, and subsequent solution of the germ and yolk; yet it is of interest, as showing that an unimpregnated ovum may advance some little distance on the road to development, and thus lends support to the theory of *parthenogenesis—i.e.*, the formation and development of ova in a female, without the intervention of a male parent. The future development of the chick takes place entirely in the area pellucida.

Fig. 332.



Section of a Blastoderm at right angles to the long axis of the Embryo after eight hours' incubation. Taken about midway between the front and hind end. A, Epiblast; B, Mesoblast; C, Hypoblast; *pr*, primitive groove; *f*, fold in the blastoderm, probably produced by the action of the chromic acid; *mc*, mesoblast cell—the line points to one of the peripheral mesoblast cells lying between epiblast and hypoblast; *bd*, formative cells. The following are the chief points represented in the section :—(1) The thickening of the mesoblast underneath the primitive groove *pr*, even when it is hardly at all present at the sides of the groove; (2) The hypoblast, C, early formed as a single layer of spindle-shaped cells; (3) The so-called segmentation cavity, in which coagulated albumen is present. On the floor of this are the large formative cells *b d*. The line of separation between the epiblast and mesoblast is too strongly marked in the figure.

In the course of a few hours after being laid, the blastoderm of the fecundated egg, in consequence of the flattening of the lower cells of the mesoblast and the development of nuclei in their interior, presents a division into three layers (Fig. 332)—an upper, middle, and inferior—termed respectively the *epiblast* (A), *mesoblast* (B), and *hypoblast* (C). Of these layers, the Epiblast, whose formation has just been traced, increases simply by fission. The origin of the Mesoderm or Mesoblast is involved in considerable obscurity.**

* According to Götte, however, the formative cells, or Dotterzellen, are formed by the segmentation of the white yolk itself. On this point, see P. Kidd, "Quarterly Journ. Microscop. Sci.," vol. xvii. (1877) p. 164.

† "Zeitsch. f. Wiss. Zool.," Band xxii.

‡ "Ann. des. Sci. Nat.," iii. Sér., "Zool." t. ii.

§ Art. 'Zeugung,' Wagner's "Handwb. der Phys.," 1853, Band iv.

‖ "Centralblatt f. die Med. Wiss.," 1869, p. 403.

¶ "Quarterly Journal of Micros. Sci.," vol. xvii. 1877, p. 160.

** In regard to the vexed question of the origin of the mesoblast, see Balfour, "Quart. Journ. Microscop. Sci.," vol. xiii. pp. 266–276, *et auct. ib. cit.*, and 'Development of Elasmobranch Fishes,' Humphry and Turner's "Journal of Anat. and Physiol.," vol. x. 1876; Allen Thomson, "Quain's Anatomy," 8th ed., vol. ii. p. 886; Kölliker, "Entwickelungsgesch. des Menschen," 2nd ed., 1879, p. 99.

According to Balfour it is produced about the sixth or eighth hour of incubation from certain cells either formative or derived from the hypoblast, which collect in the space between the epiblast and hypoblast, and these undergo a process of free cell formation to form a distinct intermediate layer. According to Edward Van Beneden,* however, at the commencement of the sixth day both the cells of the peripheral zone of the gastrodisc, where the ectodermic cells are closely applied to the endoderm, and the more deeply lying cells of the central spot are transformed into flat cells, and thus give rise to a continuous cellular layer, the hypoblast. The cells of the central layer which have not undergone this change form layers intermediate to the ectoderm and hypoblast, which is the mesoblast. The hypoblast and mesoblast are therefore derived from the primary endoderm. The first formation of mesoblast takes place in the centre of the blastoderm, where it fuses with the epiblast and forms an opaque line, the *primitive streak*. The mesoblast appears to grow at the expense of the formative cells, which travel either round or through the substance of the hypoblast; this layer is completed by the 18th–20th hour of incubation. The *Hypoblast*, the lowest of the layers of the trilaminate blastoderm, is formed by some of the cells of the endoderm becoming flattened and nucleated; it appears to grow by the direct conversion of the white yolk spheres into hypoblast cells. According to Remak the *epiblast* gives origin to the brain and spinal cord, to the special modifications of the nerves ministering to special sense, as the Retina, with its pigment layer, the Lens, Auditory hairs, Schneiderian mucous membrane, and the Epidermis, with its epithelial prolongations into the mouth, salivary ducts and cloaca, as well as the cells which form the sheath of the hair bulbs and of the sebaceous and sweat glands, and, as Ranvier has recently shown,† to the muscular coat of the sweat glands; the ascending limb of the Amnion and yolk sac, and in mammals the outer layer of the true Chorion. The *mesoblast* gives origin to the muscles, bones, connective tissues, and dermis, the cerebro-spinal and sympathetic nerves, the genito-urinary, vascular, and chylopoietic systems, and the chief substance of many glands: it also forms the outer layer of the amnion, the vascular layers of the yolk sac, the allantois and chorion, and the embryonic portions of the placenta. From the *hypoblast* originate the epithelium lining the alimentary canal (except that lining the mouth) and of the ducts of the glands connected with it, except the salivary, the epithelium of the respiratory apparatus, the deep layer of the yolk sac, and the allantois. The blastoderm now begins to spread circularly over the vitellus, so that instead of appearing as a mere disk it forms an investment for the yolk beneath the vitelline membrane, which, however, only becomes complete towards the close of the period of incubation. The bag thus produced is chiefly formed by the growth of the area opaca, but in part also, by that of the area pellucida, which gradually assumes an oval and then a pear-shape. In the centre of the area pellucida the longitudinal thickening already alluded to as the *primitive streak*, is seen about the twelfth hour; it is formed by the multiplication of the cells both of the epiblast and of the mesoblast, but chiefly of the mesoblast, and this, again, is quickly marked along the central line by an involution of the epiblast, which gives rise to the *primitive groove*‡ (*pr*, Fig. 333). This is the first indication

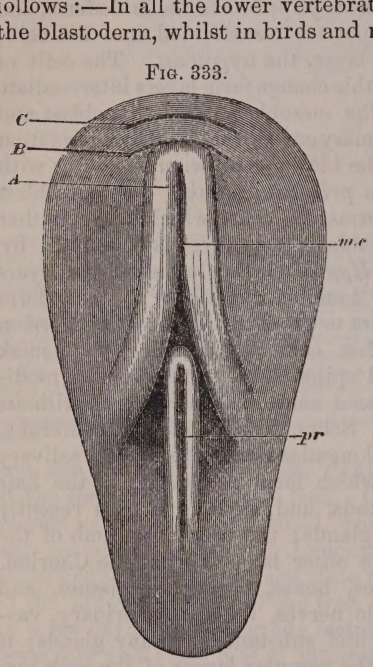
* "Archives de Biologie," tom. i. 1880, p. 219.

† "Comptes Rendus," Dec. 29, 1879.

‡ In regard to the primitive groove, see Dr. E. Dursy, "Der Primitive streif des Hühnchens, Lahr.," 1866; Balfour, 'On the Disappearance of the Primitive Groove in the Embryo

of the embryo, which in its further development is formed by a folding-off of the area pellucida from the rest of the blastoderm; the primitive groove disappears as early as the 49th hour of incubation, without entering directly into the formation of any part of the embryo; it is probably the rudiment of some ancestral stage in development which has been lost. According to Mr. Balfour the existence of the primitive groove may be explained as follows:—In all the lower vertebrates the embryo is situated at the edge of the blastoderm, whilst in birds and mammals it is situated in the centre. In the elasmobranch fishes the embryo occupies at first the normal position at the edge of the blastoderm, but in the course of its development the blastoderm grows round the yolk far more slowly in the region of the embryo than elsewhere. As a result of this unequal growth the embryo is left in a bag, the two sides of which eventually meet and coalesce in a linear fashion immediately behind the embryo. The linear streak thus formed gives rise to the primitive groove, which is consequently upon this hypothesis the last indication of a change made by the Avian ancestors in their position in the blastoderm. The first indication of the folding-off of the embryo consists in the formation of a crescentic furrow (Fig. 333, B) at a point which corresponds to the head of the embryo, and very shortly afterwards the tail and lateral folds form, which give rise more and more distinctly to the appearance of a small tubular sac seated upon and connected by a continually narrowing hollow stalk (*the vitelline duct*) with the germinal sac of the blastoderm which encloses the yolk. Soon after the appearance of the primitive streak and groove the mesoblast undergoes a cleavage into two laminæ over its whole extent, with the exception of that part which lies just beneath the axis of the embryo. The upper layer of the mesoblast unites with the epiblast, the lower layer with the hypoblast, and the yolk thus comes to have a double investment beneath the vitelline membrane. In the first formation of the head, tail, and lateral folds, both layers are equally involved, but, as shown in Fig. 334, the lower leaf is folded in more rapidly than the upper one, and a space —the *pleuro-peritoneal cavity* (*pp*, Fig. 334) appears between them. The upper or outer layer forms the *somatopleure* (*F So*), and subsequently gives rise to the body walls of the embryo. The lower or inner layer forms the *splanchnopleure* (*Sp*), and its opposite folds meeting sooner than those of the

Fig. 333.

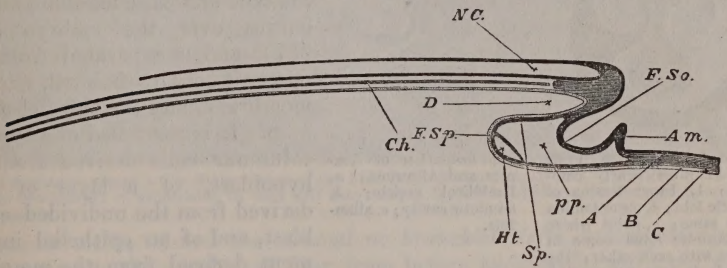


Surface view of the Pellucid Area of a Blastoderm of 18 hours. None of the opaque area is shown, the pear-shaped outline indicating the limits of the pellucid area. A, Medullary folds; B, Head fold; C, Rudimentary amnion; *me*, the medullary groove; *pr*, the primitive groove.

Chick,' "Quarterly Journ. Microsc. Sci.," vol. xiii. (1873) p. 276, and the "Development of Elasmobranch Fishes," Humphry and Turner's "Journal of Anatomy and Physiol.," vol. x. (1875), p. 682; and in a review of the second edition of Kölliker's work, ibid., pp. 790 and 791; 'On the Development of the Lacertilia together with some Observations on the Nature and Relation of the Primitive Streak,' "Quarterly Journal of Micros. Sci.," vol. xix. (1879) pp. 426–430; Kölliker, "Entwickelungsgeschichte," 1879, pp. 134–138.

upper layer, constitute the intestinal tube.* At about the 16th hour a thickening of the mesoblast occurs in front of the primitive groove, ending in front as the head fold (Fig. 333 *B*, Fig. 334). The surface of this is marked by a groove (*m c*, Fig. 333), termed the medullary groove, the sides of which constituting the *medullary folds* or *laminæ dorsales*, gradually arching over till they meet and fuse, enclose the *medullary canal.* Immediately beneath the groove the cells form a flattened cylindrical rod—the *notochord*, which is the precursor of the vertebral column (N.C., Fig. 334).

Fig. 334.



Diagrammatic Longitudinal Section through the Axis of an Embryo. *F.So.*, Fold of the somatopleure. *F.Sp.*, Fold of the splanchnopleure. The line of reference, *F.So.*, is placed in the lower bay, outside the embryo. The line of *D* is placed in the upper bay, inside the embryo; this will remain as the alimentary canal. Both folds (*F.So.*, *F.Sp.*) are parts of the head fold, and are to be thought of as continually travelling onwards (to the left) as development proceeds. *p p*, Space between somatopleure and splanchnopleure or pleuro-peritoneal cavity. *Am.*, Commencing (head) fold of the amnion. The tail fold has not yet appeared. *N.C.*, Neural canal, closed in front, but as yet open behind. The section being taken in the middle line, the protovertebræ are of course not shown. In front of the notochord is seen a mass of uncleft mesoblast, which will eventually form part of the skull. *D*, Commencing foregut, or front part of the alimentary canal. *A*, Epiblast. *B*, Mesoblast. *C*, Hypoblast. *Ht.*, Commencing heart.

Formation of Amnion and Allantois.—Coincidentally with the formation of the head fold, a second fold (Fig. 334, *A m*) appears a little in front of it, and soon others arise at the tail end and sides of the embryo, which, unlike the head fold, are formed exclusively of the somatopleure—*i.e.*, of the epiblast and a thin layer of mesoblast, and gradually rising, bend over the body of the embryo (Figs. 336, *d e;* 339, *a f*), and coalesce (*c*, Fig. 337). These are the *amniotic folds.* Each fold necessarily consists of two limbs. After their coalescence the septum disappears and two spaces exist: one which is continuous with the pleuro-peritoneal cavity between the outer and inner limbs, and one between the inner limb and the body of the

Fig. 335.

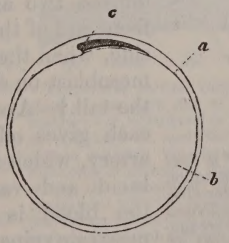


Fig. 335.—Plan of early *Uterine Ovum.* Within the external ring or zona pellucida, are the yolk sac, *a*; the yolk, *b*; and the blastoderm or incipient embryo, *c*.

Fig. 336.

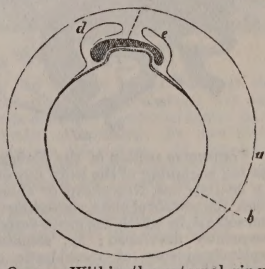


Fig. 336.—Diagram of Ovum at the commencement of the formation of the *Amnion:* *a*, chorion; *b*, yolk-sac; *c*, embryo; *d*, and *e*, folds of the somatopleure rising-up to form the amnion.

* The quadrilaminate, or secondary blastoderm thus formed, is produced in the following way (Allen Thomson's "Address," loc. cit.):—

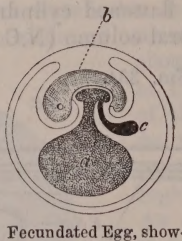
Primary blastoderm	Ectoderm		Epiblast	Secondary Blastoderm.
	Mesoderm	Somatopleure		
		Splanchnopleure		
	Endoderm		Hypoblast	

embryo. The former is the space into which the *allantois* or respiratory organ of the embryo projects; the latter is the amniotic sac, and is subsequently filled by the amniotic fluid. The allantois (Fig. 338,*c*) is not formed till the second or third day, when it appears as a bud thrown out by the splanchnopleure close to its junction with the somatopleure at the hinder end of the embryo, and gradually insinuating itself first into the pleuro-peritoneal cavity, and then between the true and false amniotic sacs, it curves over the embryo (Fig. 337), and is separated from the outer air only by the shell, vitelline membrane, and the thin false amnion. It is composed of a layer of columnar cells derived from the hypoblast, of a layer of cells derived from the undivided mesoblast, and of an epithelial investment derived from the mesoblast of the splanchnopleure.* It receives at an early period branches from the iliac arteries, which subsequently constitute the umbilical vesssels, and are developed in an extension of the mesoblast cells of the area opaca, known as the *vascular area.*

Fig. 337.

Fecundated Egg of Fowl with Allantois nearly completed: 1, Inner lamina of amniotic fold; *b*, outer lamina of the same; *c*, point where the amniotic folds come in contact with each other; the allantois is seen penetrating between the inner and outer laminæ of the amniotic fold.

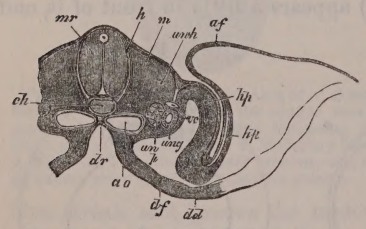
Fig. 338.



Fecundated Egg, showing formation of Amnios and Allantois: *a*, Umbilical vesicle; *b*, amniotic cavity; *c*, allantois.

The first rudiment of the *heart* in the chick appears as a solid thickening of the mesoblast of the splanchnopleure just beneath the anterior extremity of the foregut. It soon becomes hollow, and receives behind the blood of the two omphalo-mesaraic veins, which ramify over the yolk-sac, whilst in front it gives off the two aortæ, which bend round the front end of the foregut and gain its upper side, when they turn back and run in the mesoblast on each side of the notochord to the tail.† About the middle of the embryo each gives off a large omphalo-mesaraic artery, which is distributed over the pellucid and vascular areas, from whence the blood is returned by the omphalo-mesaraic veins (Fig. 344, *R. Of. A, L. Of. A.*). At the close of the first day *the protovertebræ* begin to form in the uncleft portion of the mesoblast near the middle line, which is called the vertebral plate. The first one to make its appearance is the body of third or second cervical, others soon becoming segmented off the vertebral plate both before and behind. At this time the forepart of the medullary canal with its optic and cerebral vesicles,

Fig. 339.



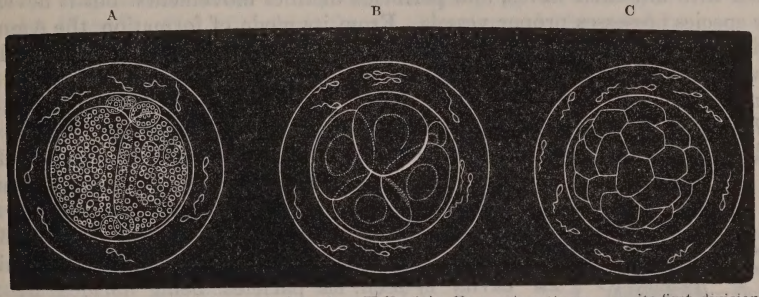
Transverse section of the *Embryo of a Fowl* at the beginning of the third day of incubation × 90–100: *ch*, Notochord or chorda dorsalis; *uwh*, the vertebral plate, consisting of undivided mesoblast, in which the proto-vertebræ are subsequently developed; *hp*, somatopleure; *df*, splanchnopleure of mesoblastic origin; *dd*, splanchnopleure of hypoblastic origin; *dr*, primitive intestinal groove; *h*, epiblast (the line in the drawing extending a little too far); *mr*, medullary tube (spinal cord); *m*, mesoblast; *p*, pleuro-peritoneal cavity; *af*, fold of the amnion; *ao*, primitive aorta; *vc*, vena cardinalis; *un*, Wolffian body; *ung*, duct of the Wolffian body.

* Dobrynin, "Wien Akad. Sitz.-ber.," lxiv. 1871, Abth. ii.

† According to Mr. Balfour ("Quarterly Journal Micros. Sci.," vol. xiii. (1873) p. 289), the cavity of the heart is produced by a splitting or absorption of the central cells of the thickened mesoblast of the splanchnopleure, whilst its muscular walls are formed from the remaining cells of the thickened portion.

which has hitherto been straight, begins to curve over the anterior extremity of the notochord, which is the commencement of the *cranial* flexure; and soon after the whole embryo becomes curved upon itself. On the third day certain

FIG. 340.

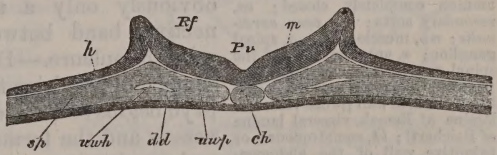


Progressive stages in the *Segmentation of the Yolk* of the Mammalian Ovum: A, its first division into two halves; B, subdivision of each half into two; C, further subdivision, producing numerous segments.

fissures or clefts, termed the *visceral* or *branchial clefts*, appear, developing in succession to the number of four from before backwards, and from within outwards. The anterior border of each forms a visceral or branchial fold, so that there are five folds. The first pair form the inferior maxillæ, and by a pair of buds they give off from their upper border the superior maxillæ. Other structures are formed in the remaining folds, which will hereafter receive mention.

735. Returning now to the development of the Mammalian ovum we find that the fine membrane covering and enclosing the blastodermic vesicle begins to show small mammillary eminences, whence the name which has been suggested for this membrane, of *Chorion primitivum* or *Membrana ovi externa*. The ovum at this period, therefore, consists of the external villous membrane or primitive chorion; of the blastodermic vesicle, composed of two layers; and of the cellular yolk. As in the Bird, the area germinativa at its first appearance has a rounded form, but it soon loses this, first becoming oval and then pear-shaped (Plate II., Fig. 11). The centre becomes clear, and constitutes the *area pellucida* (*b*), and this is bounded by a more opaque circle, the *area opaca* (*a*). The first appearance of the embryo in the form of the primitive trace with the subsequent formation of the medullary groove followed by the elevation of the *laminæ dorsales*, their junction in the middle line, and expansion anteriorly into three vesicles (Plate II., Fig. 12), afterwards to be developed into the *prosencephalon*, *mesencephalon*, and *epencephalon;* the formation of the amnion by the growth of two folds of the epiblast, and the growth of the allantois into its cavity differ in no essential respect from the similar processes in the chick, though the allantois never attains the same degree of development in the mammal. A microscopic

FIG. 341.

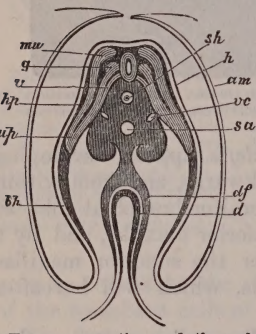


Transverse section through the *Embryo of the Chick* at the close of the first day of incubation, magnified about 100 diameters:—*ch*, notochord or chorda dorsalis; *h*, external serous layer or epiblast; *m*, medullary portion of epiblast; *Pv*, medullary groove between the dorsal laminæ *Rf* and *m*; *dd*, intestinal epithelial or glandular layer (hypoblast); *uwp*, vertebral plate, in which the primary or proto-vertebræ are formed, and which is continuous with the mesoblast, *sp*; *uwh*, fissure in the mesoblast, presenting the first indication of the pleuro-peritoneal cavity, and of the subsequent division of this layer into two other layers.

examination of the Amniotic membrane in the Human subject shows that it consists of an inner layer of tessellated epithelium, and an outer layer, which even at the fourth week presents spindle-shaped corpuscles, and at the seventh week has become well-marked connective tissue. In some animals it is provided with muscular fibres, and performs distinct movements but it never in any species possesses proper vessels. From its mode of formation, the Amnion is directly continuous with the skin of the embryo, and the Amniotic fluid in which the fœtus floats occupies the space between the inner layer and the skin.

736. As the development of the embryo progresses, the walls of the abdomen and the coats of the intestines begin to be formed by the bending downwards and forwards of the lateral portions of the blastodermic vesicle, termed respectively the *somatopleure* and the *splanchnopleure*. In Fig. 342, the mode of the development of the abdominal cavity is seen, its parietes being formed by the somatopleure, composed of the epiblast with some mesoblast (*bh*), whilst within it the deep groove of the intestines (*d*) appears, the walls of which or splanchnopleure are composed of two laminæ, the mesoblast (*df*), and the hypoblast (*d*), passing into the corresponding laminæ of the blastodermic vesicle, which already form the vitelline sac. The incipient intestine is maintained in its place by the mesentery, which begins to be formed out of a prolongation of the mass lying in front of the notochord or chorda dorsalis, in which lie the now symmetrical aorta (*sa*) and the cardinal vein (*vc*), and which is obviously only a thickened portion of the connecting band between the somatopleure and the splanchnopleure.—During the same period, a very important provision for the future support of the embryo begins to be made, by the development of Blood-vessels and the formation of Blood. Hitherto, the embryonic structure has been nourished by direct absorption of the alimentary materials supplied to it by the yolk; but its increasing size and the necessity for a more free communication between its parts than any structure consisting of cells alone can permit, call for the development of *vessels* through which the nutrient fluid may be conveyed. These vessels are first seen in *the vascular area* or that part of the germinal membrane which immediately surrounds the embryo.* In their earliest stage of development these vessels appear as *two arcus aortæ*, proceeding from the anterior part of the heart, which after a short course in the forward direction, bend backwards and run on each side of the notochord immediately beneath the aorta towards the caudal extremity. In this course, each of the primitive aortæ gives off a large vessel, the *omphalo-mesaraic artery*. At a very early

FIG. 342.



Transverse section made through the body of the *Embryonic Fowl*, near the umbilicus, on the fifth day of incubation: — *sh*, sheath of the chorda dorsalis; *h*, epiblast; *am*, amnion completely closed; *sa*, secondary aorta; *vc*, *vena cardinalis*; *mu*, muscle plate; *g*, spinal ganglion; *vr*, anterior root of the spinal nerve; *hp*, mesoblast; *up*, prolongation of the mesoblast into the abdominal wall (proto-vertebral lamina of Remak, visceral lamina of Reichert); *bh*, somatopleure, or primitive wall of the abdomen, composed of the external, serous, or epiblastic lamina, and of a layer of mesoblast; *df*, internal layer of mesoblast, in which the fibrous membranes of the intestines are developed; *d*, hypoblast. The mass around the chorda contains the vessels anteriorly, and in front, in the middle line, is prolonged as the mesentery.

* According to His (loc. cit. p. 95), Wolff, and Pander, in the chick a peripheral vessel around the germinal area, and others in the area opaca, first appear, whilst at various points small coloured masses, surrounded by a membrane or blood-islands, are developed. Both the vessels and the blood proceed directly from the white or germ-yolk. The formation of the vessels precedes that of the heart, and is quite independent of it.

period of development the two primitive aortæ unite in a single, short, symmetrical aortic tube, from which again two branches almost immediately arise, the *arteriæ vertebrales posteriores*. These, lying beneath the chorda dorsalis, extend to the posterior part of the body of the embryo, dividing ultimately into the omphalo-mesaraic, or Vitelline vessels (Fig. 344, *R.Of.A.*, *L.Of.A.*; see also Plate II., Fig. 13) which form a close network, bounded by a circular channel termed the *Vena* or *Sinus terminalis* (Fig. 344, *S.T.*). This network or vascular area soon extends itself, and the vessels finally spread over the whole of the membrane that contains the yolk. At the anterior part of the embryo the two extremities of the circular channel form the *Venæ omphalo-mesaraicæ*, which discharge their contents into the back part of the heart.—At this period the Yolk-sac is entirely separated in the Mammalia, by a constriction of the portion which is continuous with the abdomen of the embryo (Fig. 347, *b*); and it is known from that time under the name of the *Umbilical Vesicle* (Plate I., Fig. 10, *i*). The communication, however, remains open for a time through the 'vitelline duct;' and even after this has been cut-off, the trunks which connect the circulating system of the embryo with that of the vascular area are discernible. The two first veins, then, that are developed, are the Venæ omphalo-mesaraicæ, which belong not to the body of the embryo itself, but to the germinal area, and open by a short tube common to both into the posterior extremity of the Heart (Fig. 343, 1, *om*). Subsequently, by the extension of their branches over the Yolk-sac, they become the *vitelline vesssls*, still opening by two veins into the heart, and effecting the absorption of the yolk. With the formation of the intestine, however, the vessel of the right side disappears, the left alone remaining (Fig. 343, 2, *om''*), which is soon joined by a small mesenteric vessel from the intestine (Fig. 343, 3, *m*). Before this is accomplished, however, the Allantois has been developed, and to this organ two large branches pass from the Iliac Arteries, which are named *umbilical arteries;* the blood returning from it after aëration enters the two Venæ umbilicales which pass forwards and open into the common trunk of the Venæ omphalo-mesaraicæ (Fig. 343, 1, *u'u''*). The Venæ umbilicales rapidly increase in size, preponderating so much over the only remaining Vena omphalo-mesaraica, into which they originally

FIG. 343.

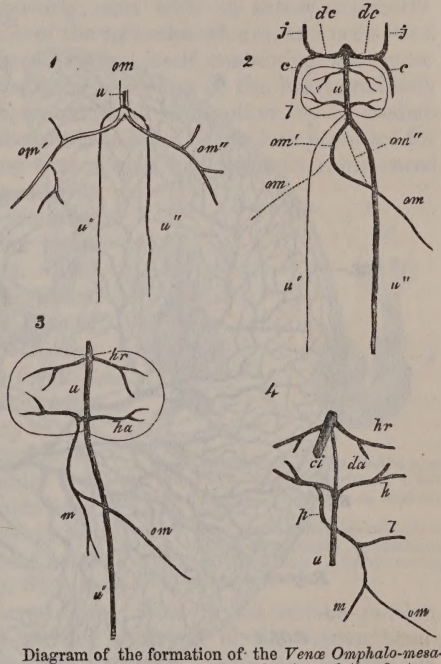


Diagram of the formation of the *Venæ Omphalo-mesaraicæ* and *Umbilicales*:—1. At the time of the first appearance of the umbilicales and the commencement of the omphalo-mesaraicæ. 2. At the time of the first appearance of the branches to and from the liver, and the diminution of the omphalo-mesaraic vessels. 3, 4. At the period of complete fœtal circulation in 1, omphalo-mesaraic trunk; in 2, 3, remains of it; in 4, vein of the yolk-sac alone; *om'* right and *om''* left vena omphalo-mesaraicæ; *u*, ductus venosus; *u'* right and *u''* left vena umbilicalis; *dc*, ductus Cuvieri; *j*, jugularis; *c*, cardinalis or Wolffian vein; *l*, liver; *ha*, hepaticæ advehentes; *hr*, hepaticæ revehentes; *m*, mesenterica; *da*, sinus venosus; *ci*, cava inferior; *p*, vena portæ; *l*, lienalis; *m*, mesenterica superior.

discharged their contents, that the latter now appears to be merely a tributary branch. As the Liver becomes developed, it surrounds the trunk of the umbilical vein, the portion thus surrounded taking the name of the *Ductus venosus* (Fig. 348, *v*), which soon forms a twofold system of tubes within that gland, the one conveying the blood to the liver, the Venæ hepaticæ advehentes; the others returning the blood from the gland substance to the umbilical vein again, and constituting the Venæ hepaticæ revehentes. The

Fig. 344.

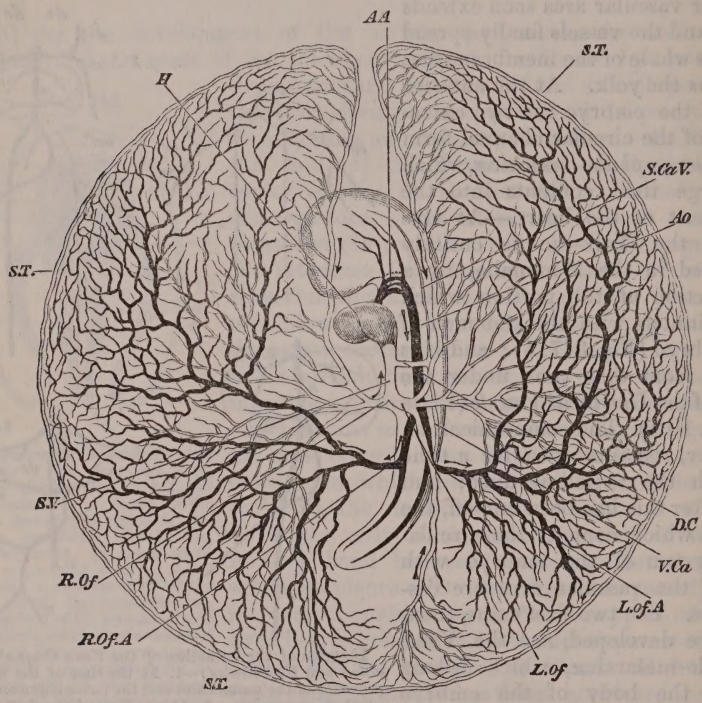


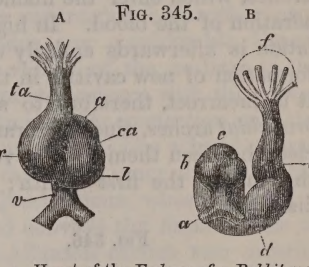
Diagram of the circulation of the Yolk Sac at the end of the third day:—*H*, Heart. *A A*, the 2nd, 3rd, and 4th Aortic Arches; the first has become obliterated in its median portion, but is continued at its proximal end as the external Carotid, and at its distal end as the internal Carotid. *Ao*, Dorsal Aorta. *R.Of.A*, and *L.Of.A*, Right and left omphalo-mesaraic arteries. *S.T.*, Sinus terminalis. *R.Of* and *L.Of*, Right and left omphalo-mesaraic veins *S.V.* Sinus venosus. *D.C*, Ductus Cuvieri. *S.Ca.V* and *V.Ca*, Superior and inferior Cardinal Veins.

right umbilical vein now disappears, and the blood returning from the placenta altogether traverses the left vein, which soon takes up a median position; the remains of the omphalo-mesaraic vessel (*om*, Fig. 343, 4), together with branches (*m*) derived from the intestine, ultimately come to open into the right *vena hepatica advehens* of the umbilical vein, and thus constitute the origin of the portal vein. That portion of the umbilical vein which lies between the two systems of hepatic branches just mentioned, remains throughout the whole of fœtal life, and is termed the Meatus venosus Arantii. It was formerly believed that the nutrient matter of the yolk passed directly through the vitelline duct, into the (future) digestive cavity of the embryo, and was from it absorbed into its structure; but there can now be little doubt, that the vitelline vessels are the real agents of its absorption, and that they convey it through the general circulating system, to the tissues in process of formation. They correspond, in fact, to the Mesenteric veins of

Invertebrate animals, which are the sole agents in the absorption of nutriment from their digestive cavity; and the blastodermic vesicle is to be regarded as the temporary stomach of the embryo—remaining as the permanent stomach in the Echinodermata.

737. The first rudiment of the Mammalian *Heart*, which is the earliest of the permanent organs of the embryo that comes into functional activity, consists, according to Kölliker,* at a period antecedent to the closure of the medullary folds of two widely separated portions lying on each side of the embryo, connected with a vein posteriorly, and with an artery anteriorly. Each half is formed by the invagination of the splanchnopleure, and is enclosed in the cervical cavity; the invaginated portion itself containing the endothelial lining. As development proceeds the two parts of the heart gradually approximate, until they are only separated from each other by a median septum. The septum is afterwards absorbed, and the heart thus possesses for a time but a single cavity. For a long time after it has distinctly commenced pulsating, and is obviously exerting a contractile force, its walls retain the cellular character, and only become muscular by a progressive histological transformation. The first appearance of the Heart in the Chick is at about the 27th hour; but the time of its formation in Mammalia has not been distinctly ascertained. In its earliest form it has the same simple character which is presented by the central impelling cavity of the lower Invertebrata, being a mere prolonged canal, which at its posterior extremity receives the veins, and at its anterior sends forth the arteries. About the 15–18th day in the Human Embryo it becomes doubly bent upon itself (Plate II., Fig. 13, *d*, and Fig. 345, A, B), one loop corresponding to the arterial, the other to the venous portion. After this, two slight enlargements (*b*) are observed in the venous bend; and the arterial bend separates into two parts by a long line of division. The two enlargements represent the auricles, and receive the venæ omphalo-mesaraicæ (*a*), which run outwards in the folds of the Splanchnopleure. Above, they open into the atrium (*c*), which leads to the right ventricle (*d*), and this again into the bulbus aortæ. The circulation is at first carried on exactly upon the plan which is permanently exhibited by Fishes. The Aorta subdivides on either side of the neck into three or four arches (Figs. 344, 350, *e*, *e'*, *e''*), which are separated by fissures much resembling those forming the entrances to the gill-cavities of Cartilaginous Fishes; and these arches re-unite to form the descending aorta, which transmits branches to all parts of the body.

FIG. 345.



A. Heart of the *Embryo of a Rabbit* seen from before:—*ta*. bulbus arteriosus; *l*, left ventricle; *r*, right ventricle; *a*, auricle; *v*, venous sinus.

B. The same heart seen from behind:—*a*, venæ omphalo-mesaraicæ; *b*, auriculæ; *c*, atrium; *d*, right auricle; *e*, bulbus aortæ, *f*, the six aortic arches.

The development of the blood-vessels has been investigated by Dr. Klein,† and by Mr. Balfour,‡ who agree in stating that they arise as a network formed by the united processes of the mesoblast cells of the Splanchnopleure. The nuclei of the cells multiply by fission; some of them become circular and acquire a yellowish colour, forming in this way the first stage in the production of a red blood-corpuscle. Others become elongated to form fusiform cells, which arrange themselves so as to enclose the

* Op. cit. pp. 289–296. † Band liii., der K. Akad. der Wiss. der Wien.

‡ "Quarterly Journ. of Microscop. Sci.," vol. xiii. (1873), p. 280.

protoplasmic processes; the processes themselves becoming liquified to form the plasma in which the corpuscles float. The formation of corpuscles occurs earliest in the central part of the hour-glass shaped pellucid area, and latest in its anterior part. The coloured corpuscles subsequently undergo increase by a process of fission which occurs within the vessels. The origin of the white corpuscles has not been clearly ascertained. The origin of the red corpuscles in Mammalian blood has recently been studied by Professor Rindfleisch,* who has been led to the conclusion that the nucleus of the red coloured cell of the red bone marrow escapes and atrophies whilst the body of the cell contracts and becomes the red corpuscle. Such is the first phase or aspect of the Circulating Apparatus, which is *common to all Vertebrata* during the earliest period of their development, and which may, therefore, be considered as its most general form. It remains permanent in the class of Fishes; and in them the vascular system undergoes further development on the same type, a number of minute tufts being sent forth from each of the arches, which enter the filaments of the gills, and are thus subservient to the aëration of the blood. In higher Vertebrata, however, the plan of the circulation is afterwards entirely changed, as will be presently described, by the formation of new cavities in the heart, and by the production of new vessels; it is incorrect, therefore, to speak of the vascular arches in *their* necks as *branchial* arches, since no branchiæ or gills are ever developed from them. The clefts between them may be very distinctly seen in the Human Fœtus towards the end of the first month; during the second, they usually close up and disappear.

FIG. 346.

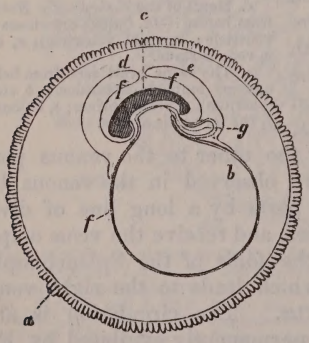


FIG. 347.

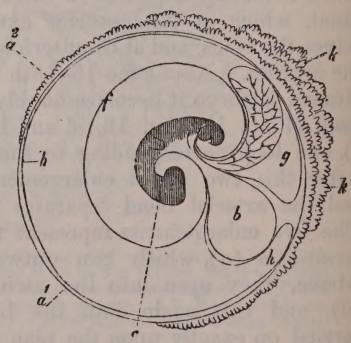


Fig. 346.—Diagram of an early *Human Ovum*, showing the *Amnion* in process of formation and the *Allantois* beginning to appear:—*a*, chorion; *b*, vitelline mass surrounded by the blastodermic vesicle; *c*, embryo; *d*, *e*, and *f*, external and internal folds of the serous layer, forming the amnion; *g*, incipient allantois.

Fig. 347.—Diagram of a *Human Ovum* in second month, showing the completion of the sac of the *Amnion*, and a further development of the *Allantois*:—*a* 1, smooth portion of chorion; *a* 2, villous portion of chorion; *k*, *k*, elongated villi, beginning to collect into Placenta; *b*, vitelline or umbilical vesicle; *c*, embryo; *f*, amnion (inner layer); *g*, allantois; *h*, outer layer of amnion, coalescing with chorion.

738. With the evolution of a Circulating apparatus, adapted to absorb nourishment from the store prepared for the use of the Embryo, and to convey it to its different tissues, it becomes necessary that a Respiratory apparatus should also be provided, for depurating the blood from the carbonic acid with which it becomes charged during the course of its circulation. The temporary

* "Archiv f. Micros. Anat.," vol. xvii. (1879), abstracts of whose Paper will be found in the "British Medical Journal," May 22, 1880, p. 789, and in the "Quarterly Journal of Micros. Sci.," 1880. See also Prof. Pouchet's paper, ibid. July, 1880.

Respiratory apparatus now to be described bears a strong resemblance in its own character, and especially in its vascular connections, to the gills of the Mollusca; which are prolongations of the external surface (usually near the termination of the intestinal canal), and almost invariably receive their vessels from that part of the system. This apparatus, which is termed the *Allantois*, sprouts forth from the splanchnopleure at the posterior extremity of the embryo and close to its junction with the somatopleure, at first as a little mass of cells, which soon exhibits a cavity (probably originating in the liquefaction of the cells of the internal part), so that a vesicle is formed (Figs. 346, 347, *g*), which looks like a diverticulum from the lower part of the digestive cavity. It appears at a very early period of fœtal life, and in the human embryo soon disappears. The outer cells are composed of mesoblast, the internal of hypoblast. This vesicle, in Birds, has been shown by Vulpian* to be possessed of a distinct contractile power, and soon becomes so large as to extend itself around the whole yolk-sac, intervening between it and the membrane of the shell, and coming through the latter into relation with the external air; but in the embryo of Mammalia, the allantois, being early superseded by another provision for the aëration of the blood, seldom attains any considerable dimensions. Its chief office here is to convey the vessels of the embryo to the Chorion; and its extent bears a pretty close correspondence with the extent of surface through which the Chorion comes into vascular connection with the decidua. Thus, in the Carnivora, whose placenta extends like a band around the whole ovum, the allantois also lines nearly the whole inner surface of the chorion; on the other hand, in Man and the Quadrumana, whose placenta is restricted to one spot, the allantois is small, and conveys the fœtal vessels to one portion only of the chorion. At first the Allantois carries two arteries and two veins, but of these the right vein soon becomes obliterated, and there remains from the fifth week to the time of birth a single vein to two arteries. When these vessels have reached the chorion, they ramify in its substance, and send filaments into its villi; and in proportion as these villi form that connection with the uterine structure which has been already described (§§ 708–714), do the vessels increase in size. They then pass directly from the fœtus to the chorion; and the allantois, being no longer of any use, shrivels up, and remains as a minute vesicle only to be detected by careful examination. The same thing happens in regard to the umbilical vesicle, from which the entire contents have been by this time withdrawn; and from henceforth the fœtus is completely dependent for the materials of its growth upon the supply it receives through the Placenta, which is conducted to it by the vessels of the umbilical cord. This state of things is represented in Figs. 348, 349, *n n'*, *o o'*.—The Allantois is commonly said to give origin to the Urinary Bladder; but this organ is really formed by an enlargement of the upper part of the uro-genital sinus (§ 746), with which the allantois communicates by a duct which gradually shrivels, only a vestige of it remaining permanent, to form the Urachus or suspensory ligament of the bladder, by which this is connected with the umbilicus. Before this takes place, however, the Allantois is the receptacle for the secretion of the Corpora Wolffiana, and also for that of the true Kidneys, when they are formed.

739. It will be seen from the succeeding diagram that the *Amnion* forms a kind of tubular sheath around the umbilical cord; it is continuous at the umbilicus with the integument of the fœtus; and at the point where the cord enters the placenta it is reflected over its internal or fœtal surface. It

* "Journ. de la Physiologie," tom. i. p. 619 *et seq.*

thus forms a shut sac, resembling that of the pleura, arachnoid, &c.; and it contains a fluid known as the *liquor amnii*, which consists of water holding in solution a small quantity of casein, kreatin, lactic acid, grape sugar,* and saline matter, and resembles, therefore, very dilute serum. At a late period of pregnancy it contains in addition, glycogen, traces of the bile salts, and urea. Like the Allantois it possesses a contractile power, owing to the unstriated muscle which it obtains from the somatopleure. During the first two months of gestation, the amnion and the inner lining of the chorion (which is really the reflected layer of the amnion, Fig. 347, *h*, just as the lining of the abdominal cavity is formed by the peritoneum) are separated by a gelatinous-looking substance; which probably aids in the nutrition of the embryo, previously to the formation of the placenta. This is absorbed during the second month; and the amnion is then found immediately beneath the chorion.—In the *Umbilical Cord*, when it is completely formed, the following parts may be traced. 1. The tubular sheath afforded by the Amnion. 2. The Umbilical Vesicle (Fig. 348, *t*), with its pedicle, or vitelline duct. 3. The Vasa Omphalo-Mesaraica (*q*, *r*), or mesenteric vessels of the embryo, by which the

Fig. 348.

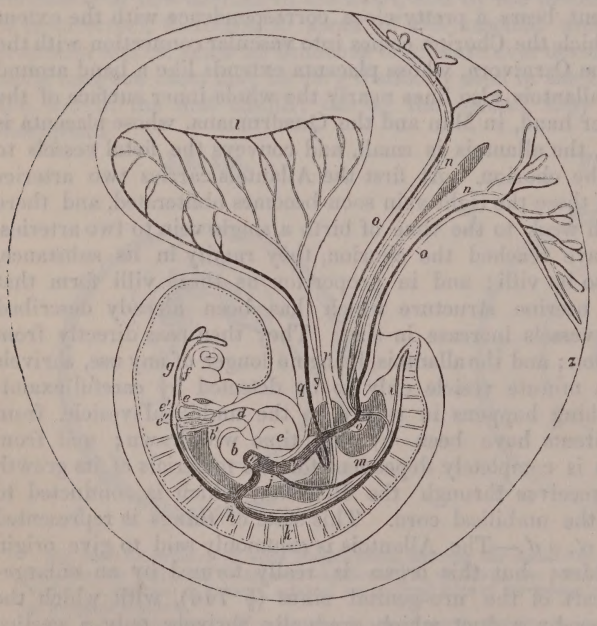


Fig. 349.

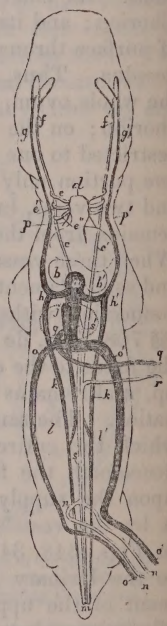


Fig. 348.—Diagram of the Circulation in the *Human Embryo* and its Appendages, as seen in profile from the right side, at the commencement of the formation of the Placenta.

Fig. 349.—The same, as seen from the front:—*a*, venous sinus, receiving all the systemic veins; *b*, right auricle; *b'*, left auricle; *c*, right ventricle; *c'*, left ventricle; *d*, bulbus aorticus; subdividing into *e*, *e'*, *e''*, Aortic arches; *f*, *f'*, arterial trunks formed by their confluence; *g*, *g'*, vena azygos superior; *h*, *h'*, confluence of the superior and inferior azygos to form the ductus Cuvieri; *j*, vena cava inferior; *k*, *k'*, vena azygos inferior; *m*, descending aorta; *n*, *n*, umbilical arteries proceeding from it; *o*, *o'*, umbilical veins; *q*, omphalo-mesaraic vein; *r*, omphalo-mesaraic artery, distributed on the walls of the vitelline vesicle, *t*; *v*, ductus venosus; *y*, vitelline duct; *z*, chorion.

yolk was absorbed into its body; these accompany the pedicle. 4. The Urachus, and remains of the Allantois. 5. The Vasa Umbilicalia (*n*, *n*, *o*), which in the later period of gestation constitute the chief part of the Cord.

* Hoppe-Seyler, "Handbuch der Chem. Anal.," 1867, p. 502.

These last vessels consist in Man of two arteries and one vein. The arteries are the main branches of the Hypogastric; and they convey to the placenta the blood which has to be aërated, and otherwise revivified, by being brought into relation with that of the mother. The vein returns this to the fœtus, and discharges a part of it into the Vena Portæ, and a part directly through the Ductus Venosus into the Vena Cava. Mr. Lawson Tait has recently made some careful investigations into the structure of the Umbilical Cord.* He believes that the growth of the cord and its spiral direction are due to a mechanism in immediate relation to the umbilical vein, and to the unequal nutrition of the cord as provided for by the varying size of the capillaries in the cord itself. Thus at some places the capillaries are only one millimetre in length, whilst at others they are 8 or 10 millimetres. As a consequence of such an unequal supply of blood, growth would result in a spiral direction. The epithelium covering the cord is continuous with the epithelium of the amniotic surface of the placenta; it consists of a single layer of irregularly polygonal nucleated cells, embedded in a thin and structureless fibrillar matrix. Wharton's jelly is composed of a number of small canals, which are probably in direct connection with the amniotic cavity. The canals are arranged in three columns, which are separated from each other, one column surrounding each blood-vessel. The substance of the cord is not nourished by the umbilical vessels which pass through it, but by a sacculated sinus, which appears to have a spiral arrangement, and extends from the omphalic ring into the substance of the cord. It gives off at short intervals thick trunks, which rapidly break up into capillaries. The blood-vessels of the cord are surrounded by the canalicular tissue which takes the place of their external coat; the arteries possess no endothelial lining, and their muscular coat is exceedingly thick. No nerve fibres have been traced in any part of the cord.

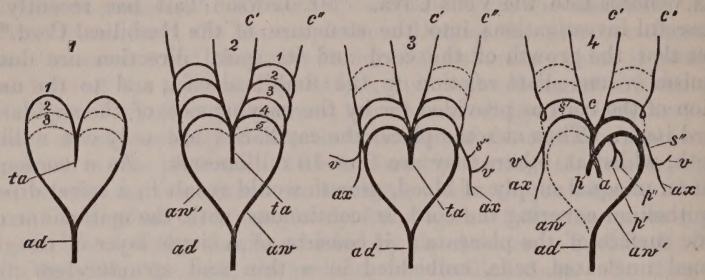
740. A change in the type of the Circulating system of the fœtus, from that at first presented by it (§ 735) takes place at a very early period. Between the fourth and eighth week the venous portion of the heart becomes much enlarged, and a septum, which arises from the lower part of the right wall, and gradually grows towards the auriculo-ventricular aperture, begins to be formed. This partition gradually divides the single ventricular cavity into two, the separation being completed at the seventh week. The septum of the auricles commences in the eighth week, as a fold, proceeding from the anterior wall, starting from the septum of the ventricles, it grows backwards towards the entrance of the sinus, stopping short of it at some distance.† It remains incomplete throughout the whole of fœtal life, the opening being termed the foramen ovale, and being guarded by the Eustachian valve. Contemporaneously with the formation of these septa, a transformation occurs in the arrangement of the Arterial trunks proceeding from the heart, which ends in the assumption of the form they present until the end of Fœtal life; and this undergoes but a slight alteration, when the plan of the circulation is changed at the moment of the first inspiration. The number of aortic arches on each side, which was five at first, soon becomes reduced in the Mammalia to three, by the obliteration of the central portions of the two highest pairs. The Bulbus Aorticus is subdivided by the adhesion of its walls at opposite points into two tubes, of which one becomes the origin of the aorta, and the other that of the pulmonary artery, and of the three remaining pairs of vascular (branchial) arches, the third being connected with the aortic trunk, contri-

* "Proceedings Royal Soc.," vol. xxiii. p. 498, and 1876, p. 417.

† Quain's "Anatomy," ed. 8, p. 788.

butes, with portions of the two highest pairs, to the formation of the external and internal carotid arteries; whilst of the second pair, the arch on the right side forms the innominate and the beginning of the right subclavian, and the other becomes the arch of the aorta, and contributes to form the left sub-

FIG. 350.



1. *Bulbus arteriosus*, with one pair of aortic arches, and dotted outlines indicating the future position of the second and third pairs. 2. *Bulbus arteriosus*, with four pairs of aortic arches and indications of the fifth. 3. *Bulbus arteriosus*, with the three posterior pairs of aortic arches, from which the permanent vessels of the embryo are developed, with dotted outlines showing the position of the two (now) obliterated anterior arches. 4. Permanent arterial trunks in their primitive form, the obliterated portions still shown in dotted outline. 1—5, primitive aortic arches; *a*, aorta; *p*, pulmonary artery; *p'*, *p''*, branches to the lungs; *aw'*, root of thoracic aorta (*ad*) on left side; *aw*, obliterated root springing from right side; *s'*, *s''*, subclavian artery; *v*, vertebral; *ax*, axillary; *c*, common carotid; *c'*, external carotid; *c''*, internal carotid. In the chick the part *s'* has been observed to atrophy, the vessel *c'* becoming the external, and *c''* the internal carotid artery.

clavian. The lowest pair is entirely obliterated on the right side. On the left, it gives off the pulmonary artery, and remains throughout fœtal life in communication with the aorta, as the Ductus Arteriosus or Ductus Botalli.*— A knowledge of these different stages in the development of the Heart and Arterial system enables us to explain many of the malformations which they occasionally present in Man; these being for the most part due to arrest of development, whereby the circulating apparatus is permanently fixed in conditions that are properly characteristic of cold-blooded animals. And it is interesting to remark, too, that the varieties which not unfrequently present themselves in the arrangement of the principal trunks given off from the Aorta, find their analogues in the arrangements that are normally characteristic of some one or other of the Mammalia.

741. The *Venous* system of the body generally undergoes changes which are even more remarkable than those of the arterial trunks. In its earliest condition, it has been ascertained by Rathke† to present essentially the same type in the embryos of all Vertebrate animals; the peculiarities of each group being acquired by a process of subsequent transformation. There is at first a pair of anterior venous trunks (Figs. 348, 349, *g g'*,) receiving the blood from the head, and a pair of posterior trunks (*k k'*), formed by the confluence of the veins of the trunk, of the Wolffian bodies, &c.; the former are persistent as the jugular veins; the latter remain separate in most Fishes, where they are designated the cardinal veins; but in Man (as in warm-blooded Vertebrata generally), they are only represented by the *venæ azygos* major and minor,‡ which coalesce into a common trunk for a considerable part of their length. One of the anterior trunks and one of the posterior unite on either side to form a canal, which is known as the Ductus Cuvieri; and the ducts of the two sides coalesce to form a shorter main canal, the sinus venosus,

* Kölliker, "Entwickelungsgeschichte des Menschen," ed. 2 (1879), p. 918.
† "Ueber den Bau und die Entwickelung des Venensystems der Wirbelthiere," 1838.
‡ See Müller's "Vergleichende Anatomie der Myxinoiden," Berlin, 1840.

which enters the auricle, at that time an undivided cavity. This common canal is absorbed into the auricle at an early period in all Vertebrata above Fishes; and after the septum auriculorum is formed, the two Cuvierian ducts, which have previously altered their position in relation to the heart, separately enter the right auricle, each being then known as a vena cava superior. This arrangement is persistent in Birds and the inferior Mammals, in which we find at a later period two Venæ Cavæ superiores, entering the right auricle separately; but in the higher Mammalia and in Man, the left duct is obliterated, with the exception of its lower extremity, which remains as the coronary sinus, and the right alone remains as the single Vena Cava superior, a transverse communicating branch being formed, to bring to it the blood of the left side.* The double Vena Cava sometimes presents itself as a monstrosity in the Human subject. The obliterated portion of the left superior vena cava can in many cases be distinguished in the adult as a fibrous cord running in the pericardium on the left auricle, and in front of the root of the left lung, and forming the *vestigial fold* of Marshall. As the anterior extremities are developed, the subclavian veins are formed to return the blood from them; and these discharge themselves into the jugulars. The Omphalo-Mesaraic vein (Fig. 349), which has been already (§ 734) shown to be formed by the confluence of the veins of the yolk-bag and intestinal canal, passes by itself, with the two Cuvierian ducts, into the auricle. The upper part of this remains to constitute the upper part of the Inferior Cava (Figs. 348, 349, *j*), the lower portion of which arises between the Wolffian bodies, and originally enters the omphalo-mesaraic vein above the liver. The Inferior Cava, which receives the hepatic vein, is gradually enlarged by the reception of most of the veins from the inferior part of the trunk and the lower extremities, and the Vena Azygos is reduced in the same proportion; in some rare cases of abnormal formation, however, the vena cava fails to be developed, and then the blood from the lower parts of the body is conveyed to the superior cava through the system of the vena azygos.

742. The following is the course of the Circulation in the mature Fœtus.—The fluid brought from the Placenta by the umbilical vein, is partly conveyed at once to the ascending Cava by means of the ductus venosus; but some branches are sent to each lobe of the liver, whilst others open directly into the vena portæ, and in either of these cases the blood reaches the vena cava inferior through the hepatic veins after it has passed through the hepatic capillaries. Having thus been transmitted through the great depurating organ, the Placenta, and the great assimilating organ, the Liver,† it is in the condition of arterial blood; but, being mixed in the great vessels with that which has been returned from the trunk and lower extremities, it loses this character in some degree by the time that it arrives at the Heart. In the right auricle, which it then enters, it would be also mixed with the venous blood brought thither by the descending Cava; were in not that a very curious provision exists to prevent (in great degree, if not entirely) any such further dilution. The Eustachian valve, which is situated at the lower margin of the vena cava inferior at the point where it opens into the right

* See the elaborate Memoirs 'On the Development of the Great Anterior Veins of Man and Mammalia' ("Phil. Trans.," 1850), by Mr. J. Marshall; who has further shown that some vestiges of the original arrangement may be traced even in the normal condition of the venous system in the adult.

† It does not seem probable that the depurating action of the Liver can be energetically performed during fœtal life; and its large dimensions and copious supply of blood appear rather to be referable to its function as a *blood-making* gland.

Fig. 351.

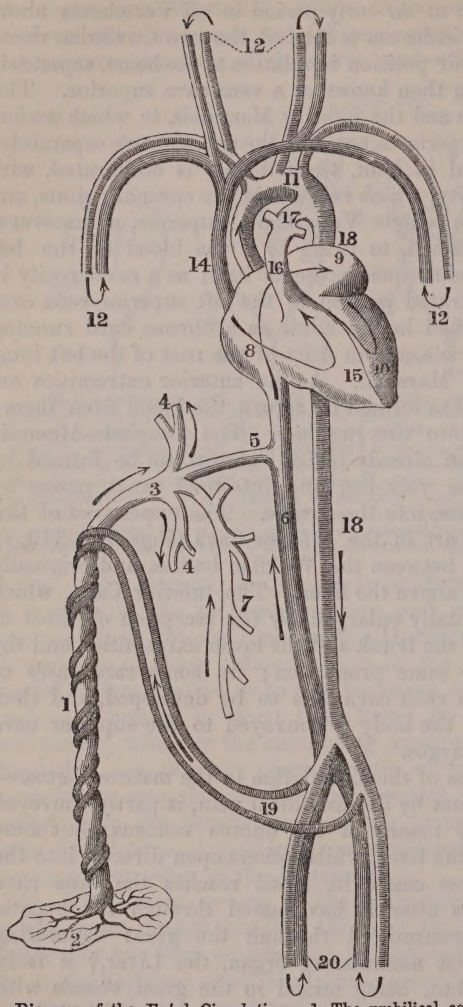


Diagram of the *Fœtal Circulation*:—1. The umbilical cord, consisting of the umbilical vein and two umbilical arteries, proceeding from the placenta (2). 3. The umbilical vein dividing into three branches: two (4, 4) to be distributed to the liver, and one (5), the ductus venosus, which enters the inferior vena cava (6). 7. The portal vein, returning the blood from the intestines, and uniting with the right hepatic branch. 8. The right auricle; the course of the blood is denoted by the arrow proceeding from 8 to 9. 9. The left auricle. 10. The left ventricle; the blood following the arrow to the arch of the aorta (11), to be distributed through the branches given-off by the arch to the head and upper extremities. The arrows (12) represent the return of the blood from the head and upper extremities through the jugular and subclavian veins, to the superior vena cava (14), to the right auricle (8), and in the course of the arrow through the right ventricle (15), to the pulmonary artery (16). 17. The ductus arteriosus, which appears to be a proper continuation of the pulmonary artery; the offsets at each side are the right and left pulmonary arteries cut off. The ductus arteriosus joins the descending aorta (18, 18), which divides into the common iliacs, and these into the internal iliacs, which become the umbilical arteries (19), and return the blood along the umbilical cord to the placenta, and the external iliacs (20), which are continued into the lower extremities. The arrows at the termination of these vessels mark the return of the venous blood by the veins to the inferior cava.

auricle, has been found, by the experiments of Dr. J. Reid,* to serve the purpose of directing the *arterial* blood, which flows upwards from the *ascending* Cava, through the foramen ovale, into the *left* auricle, whence it passes into the *left* ventricle; whilst it also directs the *venous* blood, that has been returned by the *descending* Cava, into the *right* ventricle. When the ventricles contract, the arterial blood which the left contains is propelled into the ascending Aorta, and supplies the branches that proceed to the head and upper extremities, before it undergoes any admixture; whilst of the venous blood contained in the right ventricle, part is transmitted by the Pulmonary artery to the lungs, but another (and probably by far the larger) part finds its way through the Ductus Arteriosus or Ductus Botalli into the descending Aorta, mingling with the arterial current which that vessel previously conveyed, and passing thus to the trunk and lower extremities. Hence the head and superior extremities, whose development is required to be in advance of that of the lower, are supplied with blood nearly as pure as that which returns from the placenta; whilst the rest of the body receives a mixture of this with what has previously circulated through the system. In the course of the circulation the blood is returned by the umbilical arteries to the placenta,

* "Edinb. Med. and Surg. Journal," vol. xliii.; and "Anat., Physiol., and Pathol. Researches," chap. ix.

where it gives off its carbonic acid and receives oxygen from the maternal blood. Dr. Zuntz* finds that the fœtus has less hæmoglobin (an average of 3·6 per cent.) and less available oxygen than the adult. He also shows that if the mother be asphyxiated, the fœtal blood actually loses oxygen during its passage through the placenta, as is shown by the darker colour of the blood which flows along the umbilical vein under such circumstances. At birth the course of the current is entirely changed by the cessation of the circulation through the Placenta, and by the enormous increase in the quantity transmitted to the Lungs, which takes place immediately on the first inspiration; the Ductus Venosus and the Ductus Arteriosus soon shrivel into ligaments; the Foramen Ovale becomes closed from below upwards by its valve; and the circulation which was before carried on upon the plan of that of the higher Reptiles, now becomes that of the complete Bird or Mammal.† It is by no means unfrequent, however, for some arrest of development to prevent the completion of these changes; and various malformations, involving an imperfect discharge of the function, may hence result. From the above description it is obvious that the chief propelling power in the circulation of the Fœtus is the right heart; the force of the left heart being chiefly spent in propelling a due supply of blood to the head and upper extremities; and an interesting observation of Langer‡ is in accordance with this, for he has shown that the walls of the right ventricle in the fœtus are as thick as those of the left, whilst those of the right auricle are even thicker and more muscular than those of the left auricle. This condition lasts for some days after birth, when the left heart gradually attains the superiority in thickness which is usual in adults.

Fig. 352.

Embryo of *Dog*, 25 days after last copulation:—*a*, nostrils; *b*, *b*, eyes; *c*, first visceral arches, forming the lower jaw; *d*, *d*, second visceral arches; *e*, right auricle; *f*, left auricle; *g*, right ventricle; *h*, left ventricle; *i*, aortic bulb; *k*, *k*, liver, between the two lobes of which is seen the divided orifice of the omphalo-mesaraic vein; *l*, stomach; *m*, intestine, communicating with the umbilical vesicle *n*, *n*; *o*, *o*, corpora Wolffiana; *p*, allantois; *q*, *q*, anterior extremities; *r*, *r*, posterior extremities.

743. The *Alimentary Canal* has been shown (§ 736) to have its origin in the blastodermic vesicle; being a portion pinched off (as it were) by the infolding of the splanchnopleure from that part of it which is just beneath the spinal column of the embryo, whilst the remainder, which is at that time the largest part of it, forms the vitelline or umbilical vesicle. From the folding in of the splanchnopleure its hypoblastic portion comes to line the tube, and from it is formed the epithelium of the intestine, whilst the mesoblastic portion, lying outside, gives rise to the submucous layers, muscles, glands, &c. In its earliest form it is merely part of a long narrow tube (Fig. 352, *m*), nearly straight, and communicating with the umbilical vesicle (*n*, *n*)

* Pflüger's "Archiv," Band xiv. (1877), p. 604.

† For causes of closure of the Ductus Arteriosus, see Walkhoff, Henle and Pfeiffer's "Zeitschrift," Band xxxvi. p. 109.

‡ 'Zur Anatomie der Fötalen Kreislauforgane,' "Zeits. der Gesell. d. Wien," xiii. p. 328.

at about the middle of its length; it may be regarded as composed of three divisions, an upper, middle, and a lower. The upper portion, corresponding to the foregut, comprises the Pharynx, œsophagus, stomach, and duodenum; the middle or midgut is equivalent to the rest of the small intestine and to the upper part of the colon; the lowest part or hindgut forms the lower part of the colon and the rectum. At first, neither mouth nor anus exists. The mouth is formed by an involution of the facial portion of the embryo, and is therefore lined at first with epiblast; it appears about the sixth week. The anus is a longitudinal slit which opens below the external organs of generation about a week after the appearance of the mouth. The tube gradually manifests a distinction into its special parts, œsophagus, stomach, small intestine, and large intestine; and the first change in its position occurs in the stomach, which, originally disposed in the line of the body, afterwards takes an oblique direction. The curves of the large and small intestine present themselves at a later period. It is at the lower part of the small intestine, near its termination in the large, that the entrance of the vitelline duct persists; and a remnant of this canal is not unfrequently preserved throughout life, in the form of a small pouch or diverticulum from that part of the intestine. Villi appear in both the large and small intestine about the fourth month, but they soon become rudimentary in the large intestine, in which they can no longer be distinguished after the eighth month. In the small intestines the villi are permanent.

744. In immediate connection with the intestinal tube we find the first rudiments of the *Liver*, which is formed in the chick at about the 60th hour of incubation by the thickening of the meso- and hypoblastic cells in the wall of the duodenum, at the spot at which the hepatic duct is subsequently to discharge itself. This thickening (Fig. 353), which is situated a little behind the heart, soon presents two diverticula which embrace the meatus venosus or united trunk of the omphalo-mesaraic veins, which, as it passes between them, exhibits numerous small bulgings. Towards the end of the third day, according to Foster and Balfour, there may be observed in the greatly thickened mesoblastic investment of each diverticulum a number of solid cylindrical masses of cells which are apparently outgrowths from the hypoblast of the diverticulum. These unite and form a network; the mesoblast contained in the meshes becoming at the same time largely converted into blood-vessels. In addition to this network of solid hypoblastic cylinders, the diverticula also send out hollow processes lined with hypoblast. On the fourth day the two masses meet beneath the meatus venosus. The blood-vessels of the mesoblast enter into communication with the meatus venosus. "It may soon be observed that in those vessels which are connected with the posterior part of the liver, the stream of blood is directed from the meatus venosus into the network of the liver, and they are therefore known as the venæ advehentes. In those connected with the anterior part—the venæ revehentes—the reverse is the case; here the blood flows from the liver into the meatus venosus. The thick network of solid cylinders represents the hepatic parenchyma of the adult liver, while the hollow processes of the

Fig. 353.

Origin of the *Liver* from the intestinal wall in the embryo of the Fowl, on the fourth day of incubation: —*a*, heart; *b*, intestine; *c*, everted portion giving origin to liver; *d*, liver; *e*, portion of vitelline vesicle.

diverticula are the rudiments of the biliary ducts."* As this is going on, the hepatic mass is gradually removed to a distance from the wall of the alimentary canal; and the cæcum is narrowed and lengthened, so as to become a mere connecting pedicle, forming, in fact, the main trunk of the hepatic duct.—In the Human embryo, the formation of the Liver begins at about the third week of intra-uterine existence; the organ is from the first of very large size, when compared with that of the body; and between the third and fifth weeks it is one-half the weight of the entire embryo. It is at that period divided into several lobes. By the third lunar month the liver extends nearly to the pelvis, and almost fills the abdomen; the right side now begins to gain upon the left; the gall-bladder makes its first appearance at this time. The subsequent changes chiefly consist in the consolidation of the viscus, and the diminution of its proportional size. Up to the period of birth, however, the bulk of the liver, relatively to that of the entire body, is much greater than in the adult; the proportion being as 1 to 18 or 20 in the new-born child, whilst it is about 1 to 36 in the adult; and the difference between the right and left lobes is still inconsiderable. During the first year of extra-uterine life, however, a great change takes place; the right lobe increases a little or remains stationary, whilst the left lobe undergoes an absolute diminution, being reduced nearly one-half; and as, during the same period, the bulk of the rest of the body has been rapidly increasing, the proportion is much more reduced during that period than in any subsequent one of the same length. According to Meckel the liver of the newly-born infant weighs one-fourth heavier than that of a child eight or ten months old; and as the weight of the whole body is more than doubled during the same time, it is obvious that the change in the proportion of the two must be principally effected at this epoch. The liver seems to be engaged during fœtal life in the depuration of the blood (as appears from the accumulation of *meconium*, which is chiefly altered bile mixed with the secretion of the alimentary canal and a few desquamated epithelial cells in the intestinal canal at birth); but at the same time it is serving as a blood-making organ, containing many free nuclei and protoplasmic masses,† and this is probably its principal function before birth. The general history which has just been given of the development of the Liver, seems equally applicable to the other glands that are evolved from the mesoblast and hypoblast forming the parietes of the Alimentary canal, such as the *Pancreas*, mucous and Peptic glands;‡ as well as the salivary glands, although they are developed from the mesoblast and epiblast, since they all seem to commence in little masses of cells, formed by an increased development, at certain spots, of the layers of blastema which originally constituted its wall; and whilst the cells of the mesoblast give origin to the proper vesicles of each gland, its ducts and tubuli, those of the hypoblast or epiblast form their epithelial lining.—The development of the *Spleen* and of the *Adrenal*, *Thymus*, and *Thyroid* bodies, have been already described.

745. The *Lungs* are also developed from the mesoblast in immediate relation with the upper part of the Alimentary canal, their rudiments, which form the primary bronchi, shooting-forth as a pair of bud-like processes (Fig. 354, *a*) from the under or anterior surface of the œsophageal portion. These were originally and correctly described by Von Baer as hollow, and as

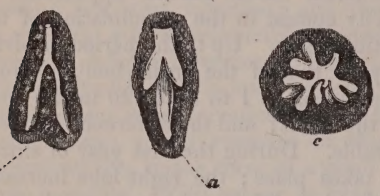
* Foster and Balfour's "Elements of Embryology" (1874), p. 132.

† Schenk, "Centralblatt," 1869, p. 865.

‡ See Schenk, "Anat. Phys. Untersuch. Wien," 1872. Abstract in "Centralblatt," 1873, p. 35.

being in reality *diverticula* from the tube itself. Like it, they consist of mesoblast lined by hypoblast. They gradually increase in size, and frequently divide, extending downwards by the multiplication of their component cells in that direction; and their cavities at first communicate with the pharynx by separate apertures; these, however, as the channels are elongated into tubes, coalesce to form the trachea, and the pulmonary organs become removed to a distance from their point of exit (Fig. 354, *b*).—The first appearance of the Lungs in the Chick takes place towards the close of the third day, and in the Human embryo at about the sixth week. Their surface soon becomes studded with numerous little wart-like projections, which are caused by the formation of corresponding enlargements of their cavity; these enlargements speedily become prolonged, and develop corresponding bud-like enlargements from their sides; and in this manner the form of the organs is gradually changed, a progressive increase in their bulk taking place from above downwards, in consequence of the extension of the bronchial ramifications of the single tube at the apex. At the same time, however, a corresponding increase in the amount of the parenchymatous tissue of the lung is taking place; for this is deposited in all the interstices between the bronchial ramifications, and might be compared with the soil filling up the spaces amongst the roots of a tree. It is in this parenchyma that the pulmonary vessels are distributed; and the portion of it which extends beyond the terminations of the bronchial tubes seems to act as the nidus for their further extension. It can be easily shown that, up to a late period of the development of the lungs the dilated terminations of the bronchi constitute the only air cells (Fig. 354, *c*); but, as already mentioned, the parenchyma subsequently has additional cavities formed within it.—It is a fact of some interest, as an example of the tendency of certain diseased conditions to produce a return to forms which are natural to the fœtal organism, or which present themselves in other animals, that up to a late period in the development of the Human Embryo, the lungs do not nearly fill the cavity of the chest, and the pleura of each side contains a good deal of serous fluid.

Fig. 354.



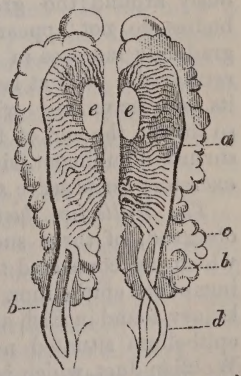
First appearance of the *Lungs*:—*a*, in a *Fowl* at four days; *b*, in a *Fowl* at six days; *c*, termination of bronchus in a very young *Pig*.

746. The embryological development of the *Urinary* organs in Vertebrate animals is a subject of peculiar interest;* owing to the correspondence which may be traced between the transitory forms they present in the higher classes, and their permanent condition in the lower. In this respect there is an evident analogy with the Respiratory system. The first appearance of any-

* Special attention has recently been devoted to this subject, more especially by Dr. Gasser, "Arch. f. Mikr. Anat.," vol. xiv. An abstract of this Paper will be found in the "Quarterly Journal of Microscop. Sci.," vol. xix. (1877), p. 16. Prof. Semper, "Centralbl. f. d. med. Wiss.," 1874, pp. 544, 817, 927 and 945. Dr. Alex. Schultz, *ibid.* 1874, p. 804; Dr. Sernoff, *ibid.* 1874, p. 481; an abstract of these Papers will also be found in the same Journal, vol. xv. (1875), pp. 91–94. Mr. Balfour 'On the Origin and History of the Urino-genital Organs of Vertebrates,' Humphry and Turner's "Journal of Anat. and Physiol.," vol. x. (1876), p. 17, where a bibliography of the subject up to that year is given; "Monograph of Elasmobranch Fishes;" 'On the existence of a head kidney in the embryo chick, and on certain points in the development of the Müllerian duct,' "Quart. Journ. Micros. Sci.," vol. xix. (1879), p. 1; Mr. Adam Sedgwick, 'Development of the kidney in its relation to the Wolffian body,' *ibid.*, vol. xx. (1880), pp. 146 and 373. From the latter Papers most of the statements in the text have been taken.

thing resembling a Urinary apparatus in the Chick is seen, according to Dr. Gasser, in an embryo with eight protovertebræ, as a slight projection from the intermediate cell mass towards the epiblast in the region of the three hindermost protovertebræ. In the next stage, with eleven protovertebræ, the solid rudiment of what will afterwards become a duct extends from the fifth to the eleventh protovertebra, from the eighth to the eleventh protovertebra it lies between the epiblast and mesoblast, and is quite distinct from both. In the region of the fifth protovertebra, where the duct was originally continuous with the mesoblast, it has now become free, but is still attached in the region of the sixth to the eighth protovertebra. In an embryo with fourteen protovertebræ the duct extends from the fourth to the fourteenth protovertebra, and is now free between the epiblast and mesoblast along its whole extent. It is still for the most part solid, though perhaps a small lumen is present in its centre. In the succeeding stages the lumen of the duct, which is formed by the cells assuming a radiating arrangement, and separating at their common point of junction, extends backwards and forwards. The duct itself also passes inwards till it acquires its final position close to the peritoneal epithelium, at the same time its hinder end elongates till it comes into connection with the cloacal section of the hind gut. On the second half of the third day, therefore, the duct appears as a long canal, extending on each side of the spinal column, from the region of the heart, towards the allantois (Fig. 352, *o*, *o*), seen also in transverse section in Fig. 339, *ung* ; on the sides of this are a series of elevations and depressions, indicative of the incipient development of cæca. On the fourth day the *Corpora Wolffiana*, as they are then termed, are distinctly recognized as composed of a series of cæcal appendages, which are attached along the whole course of the first-mentioned canal, opening into its outer side (Fig. 355, *a*). On the fifth day these appendages are convoluted, and the body which they form acquires increased breadth and thickness; they evidently then possess a secreting function, and the fluid which they separate is poured by their long straight canals (*b*, *b*) into the two horns of the cloaca; and between their component shut sacs numbers of small points appear, which consist of little clusters of convoluted vessels, exactly analogous to the Corpora Malpighiana of the true kidney. Mr. Sedgwick states that the Wolffian body develops first of all in the front portion of the embryo, and that it then passes gradually backwards. The tubules of the Wolffian body do not develop from serial involutions of the peritoneal epithelium, but from the cells of the intermediate cell mass, independently of the Wolffian duct, into which they only open at a later date. The cell mass is a group of cells stretching between the protovertebræ and the dorsal inner angle of the body cavity (Fig. 339); it is at first continuous with the peritoneal epithelium, but afterwards breaks away from it, and forms a cellular blastema, which lies just internal to the Wolffian duct, and may be called the Wolffian blastema. The Wolffian blastema almost directly breaks up into certain structures which represent the first rudiments of the Wolffian tubules. These tubules are formed by the appearance, just internal to the Wolffian duct, of a number of vesicles which are either oval or circular, and are lined by columnar cells. From the inner and dorsal wall of the vesicles a glomerulus

Fig. 355.



State of the *Urinary* and *Genital Apparatus* in the early embryo of the Bird :—*a*, corpora Wolffiana; *b*, *b*, their excretory ducts ; *c*, kidneys; *d*, ureter; *e*, *e*, testes.

is afterwards developed, the whole structure grows enormously, and gives rise to the Malpighian body, and to the complicated coils of the later Wolffian tubule, which opens into the Wolffian duct. At a slightly later stage, secondary, tertiary, &c., tubules arise in a similar manner, from small masses of cells, each being placed dorsally to the last formed tubule.

The Wolffian bodies remain as the permanent urinary organs of Fishes; but in the higher Vertebrata they give place to *the true Kidneys*, the development of which commences in the Chick about the sixth day, only a small part persisting in the male as the epididymis. The Wolffian blastema, already mentioned, gives rise, for a certain distance, to the Wolffian tubules. In the Chick this extends as far back as the thirtieth protovertebra, but beyond this point—*i.e.*, from the thirty-first to the thirty-fourth segments inclusive—the blastema gives origin to the epithelium of the permanent kidneys, and it is therefore known between these limits as the kidney blastema. During, and for some time after, the formation of the Wolffian body, the kidney blastema remains perfectly quiescent. About the 80-100th hour, however, the ureter or duct of the permanent kidney arises as a growth forward from the dorsal border of the enlarged end of the Wolffian duct. The kidney blastema is now found close to the body cavity, lying dorsally to its former position, just internal to the dorsal extremity of the dilated Wolffian duct. At the end of the fifth day the ureter acquires a greater development, and overlaps the hind end of the Wolffian body; the kidney blastema becoming completely separated from the Wolffian body, and investing the anterior extremity of the ureter. By the seventh day the ureter, which is now a small duct lying just dorsal to the Wolffian body, and opening separately into the cloaca, has increased in length, and has become dilated at intervals, whilst the kidney blastema has collected round these dilatations. The dilatations put out tubules which burrow into the kidney blastema, which thereupon arranges itself most conspicuously around the growing extremities of the tubules. The Malpighian bodies do not appear distinctly till after the eighth day. As the kidneys gradually increase in size and advance in development, the Wolffian bodies retrograde, until at last only the anterior or so-called sexual portion persists, its tubules uniting with the seminiferous tubules to form the epididymis, so that at the end of fœtal life, the only vestige of them is to be found as a shrunken rudiment, situated (in the male) near the testes, to which their excretory ducts serve as the outlets, becoming the 'vasa deferentia.'

The Müllerian duct consists, at the earliest period at which it has been observed, of three successive open involutions of the peritoneal epithelium, which are connected together by more or less well-defined ridge-like thickenings of the epithelium. It corresponds, according to Mr. Balfour,* to the head kidney found in Fish and Amphibia, and it arises from that layer of thickened epithelium situated near the dorsal angle of the body cavity, close to the Wolffian duct, which is known as the germinal epithelium. The anterior of the three open grooves is simply a shallow groove in the thickest part of the germinal epithelium, and lies some little distance behind the front end of the Wolffian duct; its walls become gradually continued into a slight ridge-like thickening of the germinal epithelium, and the same description applies to the second and third grooves. At a later stage the ridges separating these grooves become better marked, and are perforated to form ducts connecting the adjacent grooves. At a still more advanced period of development the ridges become more or less completely detached from the peritoneal epithelium, and the whole head kidney then consists of a slightly convoluted duct, with at

* Op. cit. p. 2.

least three peritoneal openings, which is continued posteriorly into the Müllerian duct. Still later the head kidney atrophies, its two posterior openings vanish, and its anterior opening remains as the permanent opening of the Müllerian duct. These changes are usually accomplished between the 90th and 120th hours of incubation. The head kidney of the Chick possesses also a paired glomerulus similar in its structure to that found in the head kidney of the Amphibia. Before the head kidney has disappeared, the rudiment of the Müllerian duct consists of a solid rod of cells continuous with the third groove of the head kidney, and terminating by a fine point of about two cells, wedged in between the Wolffian duct and the germinal epithelium. When the atrophy of the head kidney is almost complete, the Müllerian duct extends nearly to the cloaca, and the lumen is continued close to its terminal point, the duct terminating by fusing with the walls of the Wolffian duct. At the close of the sixth day the Müllerian duct, as it passes backwards, is in contact with the wall of the Wolffian duct on one side and with the germinal epithelium on the other. It gradually dilates; the external wall of the Wolffian duct becomes greatly thickened, and pushed in at its middle part so as to touch the opposite wall of the duct and form a bay, in which the Müllerian duct lies. No well-defined line of separation can then be traced between the walls of the Wolffian and those of the Müllerian ducts, but between the two there is a narrow clear space traversed by an irregular network of fibres, in some of the meshes of which nuclei are present. The Müllerian duct ultimately opens separately, and above the Wolffian duct, into the cloaca. If these observations be correct, it will be seen that the views previously held as to the origin of the Müllerian duct in a space between a portion of the thickened germinal epithelium and the Wolffian duct, but quite independently of both of them, is no longer tenable. The duct of Müller on the right side (in the Fowl, the left with the corresponding ovary disappearing) is never closed-in in front, and remains in the female as the oviduct. In the male it is almost entirely obliterated on both sides. The history of the development of the Urinary organs in the human embryo seems to correspond closely with the foregoing. The Wolffian bodies begin to appear towards the end of the first month; and it is in the course of the 7th week that the true Kidneys first present themselves. When at their greatest development, the Corpora Wolffiana are the most vascular parts of the body next to the liver; four or five branches from the aorta are distributed to each, and two veins are returned from each to the vena cava. The upper arteries and their corresponding veins are afterwards converted into the Renal or emulgent vessels; and the lower into the Spermatic vessels. From the beginning of the 3rd month, a diminution takes place in the size of the Wolffian bodies, *pari passu* with the increase of the Kidneys; and at the time of birth scarcely any traces of the former can be found. At the end of the 3rd month, the Kidneys consist of seven or eight lobes, the future pyramids; their excretory ducts still remain in the canal, the *sinus urogenitalis*, which receives those of the Wolffian bodies (subsequently to become the vasa deferentia), and of the Fallopian tubes;* and this opens, with the rectum, into a sort of *Cloaca*, analogous to

* Although it has been usually considered that the Vasa Deferentia of the male and the Fallopian tubes of the female are homologous organs, yet this is not really the case; for the former are derived from the excretory ducts of the Wolffian bodies, whilst the latter are independent formations, which are found to co-exist with seminal ducts at an early period of development, alike in male and in female embryos. (See Kobelt, "Der Nebeneierstock des Weibes," Heidelberg, 1847.) The ducts of the Wolffian bodies, although subsequently disappearing in the females of most Mammals, remain permanent as 'Gaertner's canals' in the female Ruminants and Pig.

that which is permanent in the oviparous Vertebrata. The Kidneys are at this time covered by the Adrenals, which equal them in size; about the 6th month, however, these have decreased, whilst the kidneys have increased, so that their proportional weight is as 1 to $2\frac{1}{2}$. At birth the weight of the Kidneys is about three times that of the Adrenals, and they bear to the whole body the proportion of 1 to 80; in the adult, however, they are no more than 1 to 240. The lobulated appearance of the kidney gradually disappears; partly in consequence of the condensation of the areolar tissue which connects its different portions, and partly through the development of additional tubuli in the interstices.—*The Urinary Bladder* is formed quite independently of the secreting apparatus, being an enlargement of the lower portion of the Allantois, a constricted part of the same fœtal organ, forming the commencement of the urethra in the male, and the whole length of that canal in the female (§ 748).

747. The essential parts of the *Generative Apparatus*—namely, the Testes in the male, and the Ovaria in the female—are first developed in such immediate proximity with the Corpora Wolffiana (Fig. 355, *e*, *e*), that they have been supposed to sprout forth from them; this, however, is not really the case, as they have an independent origin in the intermediate mass of mesoblastic blastema (termed by Foster and Balfour the *genital ridge*), from which the Wolffian body and Kidneys have successively been differentiated. They make their first appearance in the Chick, as delicate striæ on the Wolffian bodies, about the fourth day; at which period no difference can be detected between the Testes and the Ovaria, which originate in precisely the same manner. The superficial cells proceeding originally from the epiblast acquire special characters, and, as already described (§ 696), become invested and enclosed by an outgrowth of the stroma of the ovary, and constitute the primordial ova. In the Human embryo, the rudiments of the sexual organs—whether testes or ovaria—first present themselves soon after the kidneys make their appearance, that is, towards the end of the 7th week. They are originally much prolonged, and seem to consist of a kind of soft homogeneous blastema, in which the structure characteristic of each organ subsequently develops itself. The *Testis* gradually assumes its permanent form; the epididymis appears in the 10th week; and the gubernaculum (a membranous process from the filamentous tissue of the scrotum, analogous to the round ligament arising from the labium, and attached to the ovary in the female), which is originally attached to the vas deferens, gradually fixes itself to the lower end of the testis or epididymis. The Wolffian ducts remain as the vasa deferentia of the male (§ 746), the vesiculæ seminales being developed as diverticula from their posterior extremity. The Testes begin to descend at about the middle of pregnancy; at the seventh month they reach the inner ring; in the eighth they enter the passage; and in the ninth they usually descend into the scrotum. The cause of this descent is not very clear: it can scarcely be due merely, as some have supposed, to the contraction of the gubernaculum; since that does not contain any muscular structure until after the lowering of the testes has commenced. It is well known that the testes are not always found in the scrotum at the time of birth, even at the full period. Upon an examination of 97 new-born infants, Wrisberg found both testes in the scrotum in 67, one or both in the canal in 17, in 8 one testis in the abdomen, and in 3 both testes within the cavity. Sometimes one or both testes remain in the abdomen during the whole of life; but this circumstance does not seem to impair their function.* This condition is natural, indeed, in the Ram.

* A case occurred within the Author's knowledge, in which both testes remained in the abdomen until the tenth year, and then descended.

According to Waldeyer,* the first appearance of *the ovary* consists of a thickened germ epithelium, investing a small vascular outgrowth, rich in cells, which projects from the interstitial tissue of the Wolffian body on its median side, and which subsequently forms the stroma of the ovary. The germ epithelium itself is derived by direct proliferation from the columnar cells which invest the median side or surface of the Wolffian body, and which are continuous with the layer of columnar cells lining the pleuro-peritoneal cavity of the embryo in the early stages of development. In a fœtus of 7½ months, Dr. Foulis found that the germ epithelium thus formed consists of columnar cells lying side by side, and so arranged as to form an investment to the whole ovary. The germ epithelium rests upon a thin irregular layer of connective tissue, which forms part of the general stroma of the ovary, and is the forerunner of the tunica albicans. The ovary at this period consists of a stroma attached to a stalk of fibro-vascular tissue, which is covered by an epithelium continuous on the one side with the peritoneal epithelium, and on the other with the germ epithelium. If the germ epithelium be examined at this period, the cells which compose it will be found to consist of nucleated masses of protoplasm, varying in size, at first somewhat columnar, afterwards oval or spherical. As development proceeds, the nucleus of one of the larger germinal epithelium cells swells up, and becomes first oval, then spherical, and marked with a double contoured line, within which one or two nucleoli are generally seen, whilst around it is produced gradually that protoplasm which assumes such dimensions in this the primordial ovum. In contact with the primordial ova are small fusiform cells, some of which appear to have grown up amongst the germ epithelium from the stratum of connective tissue upon which this epithelium rests. The primordial ova are developed in groups, each group becoming enclosed in the connective tissue of which the stroma of the ovary is composed. After the cells have been included in meshes of the stroma, they increase in number and size, and thus results the formation of those large egg-clusters which are found under the germinal epithelium in all parts of the ovary. In each egg-cluster, however, certain cells are found to be much farther advanced than others, and these alone reach maturity, the smaller cells, although potentially ova, abort and disappear, some probably forming nourishment for the more vigorous and healthy ones, whilst others, as will be afterwards shown, give rise to the follicular epithelium. According to Balfour, whose observations are supported by Klein, the primordial ova are formed by a segregation taking place in the contents of the nucleus within the membrane, the granular contents passing to one side, where they form an irregular mass, whilst the remaining space within the membrane is perfectly clear. The granular mass gradually develops itself into a beautiful reticulum with two or three highly refracting nucleoli, one of which eventually becomes the largest and forms the germinal spot. At the same time the body of the ovum becomes slightly granular. While the above changes, more especially those involving the nucleus, are taking place, the protoplasm of two or more ova may fuse together, and multi-nucleated masses may thus be formed. The whole of such a multi-

* Foulis, 'On the Development of the Ova and Structure of the Ovary in Man and other Mammalia,' "Trans. Roy. Soc. Ed.," vol. xxvii., from whose monograph we take most of the account given in the text; and also in Humphry and Turner's "Journal," vol. xiii. (1879), p. 352, 'On the structure of the Ovary.' For recent Memoirs on the subject, see Balfour's Paper 'On the Structure and Development of the Vertebrate Ovary,' in the "Quart. Journ. Micros. Sci.," vol. xviii. (1878), p. 418, an abstract of which will be found in Klein and Noble's "Atlas of Histology," 1880, p. 291.

nucleated mass is sometimes connected into a single ovum, in which case all the nuclei except one, atrophy; in other cases, the mass gives rise by subsequent division to two or more ova, each with a single germinal vesicle. At a later period than the one above described, the stroma of the ovary grows into the egg-clusters, and separates the primordial ova, enclosing each in a separate capsule. The first *Graafian follicle* is thus formed, consisting at this stage of a young ovum, which completely fills the follicle of stroma surrounding it. Some of the smaller cells which accompanied the larger ones in the egg-clusters, and which like them originated from the cells of the germinal vesicle, surround the primordial ovum, and give rise to the follicular epithelium.* The cells constituting this epithelium are flat, circular, or oval plates, which appear to be fusiform in section, and which at first form a single layer surrounding the ovum as with a wreath. From these cells is derived the *membrana granulosa;* at first a single layer, it soon consists of several layers, owing to the rapid multiplication of the first cells by fission. At a later stage, some of the cells in the intermediate layer break down and dissolve. In this way a space is formed, which is afterwards filled with the *liquor folliculi.* This solution of cells does not take place throughout the whole circle of the ovum, which therefore remains attached at one point to the wall of the follicle, and from this point a layer of the membrana granulosa or follicular epithelium extends over the ovum as the *discus proligerus. The zona pellucida* or *vitelline membrane* is formed by a hardening of the outer portion of the yolk, and is not, as was supposed by Reichert, Pflüger, and Waldeyer, a product of the follicular epithelium. At birth, the most advanced ova are met with deep in the ovary. After birth, the cells of the germinal epithelium gradually become smaller and lose their columnar form, so that at the age of six years they present the appearance of small flattened hexagonal cells, which can readily be stripped off the surface of the ovary. After the age of two and a half years the ova are formed in the human ovary.—The *Ovary* undergoes much less alteration in its position than do the testes. Its efferent canal (which, as just stated, is *not* the representative of the vas deferens of the male, but is the duct of Müller) remains detached from it, presents a free terminal aperture, and constitutes the Fallopian tube. The *uterus* and *vagina* are formed by the coalescence of the lower portions of the Müllerian ducts, the upper portion of the ducts remaining permanently as the Fallopian tubes. By the subsequent absorption of the septum in the coalesced portions, the genital canal is formed. In the Female, this canal increases in size; and a marked separation is established about the fifth or sixth month by means of a transvere dismemberment between its lower or vaginal portion and its upper or uterine portion. The former opens into the uro-genital sinus, it commences at the vestibule, and receives the terminations of the urethra and of the Wolffian ducts, remaining permanently unclosed. In the Male, on the other hand, no such transverse dismemberment of the genital canal ever takes place; it makes no advance in development, and diminishes in relative size; so that at the period of fœtal maturity it is only discoverable as the *vesicula prostatica,* which has been supposed until recently to be an appendage to the prostate gland. A transverse con-

* Foulis is opposed to Waldeyer, Balfour, and other observers on this point, for he believes that "small fusiform cells belonging to the stroma of the ovary, and situated in the wall of the follicle, indent the protoplasm of the young ovum as it lies in its capsule," and that in a ripe Graafian follicle the stroma cells outside the membrana propria folliculi become converted into cells exactly similar to the true follicle cells, so that it is possible to trace the ordinary stroma cells outside the follicle through all stages of development into cells exactly resembling the follicle cells. This last observation affords to Dr. Foulis the most conclusive proof of the origin of the follicle cells from the ordinary cells of the stroma.

striction in this canal marks out its vaginal from its uterine portion; the former having exactly the same relation as in the female to the terminations of the urethra and of the Wolffian ducts (vasa deferentia) in the 'uro-genital sinus,' which is subsequently closed in, however, so as apparently to form a continuation of the urethral canal; and the latter, in those Mammals whose females have a 'uterus bicornis,' exhibiting a like divarication into two lateral halves.*

748. The history of the development of the *external Organs of Generation* in the two sexes presents matter of great interest, from the light which is thrown by a knowledge of it upon the malformations of these organs, which are among the most common of all departures from the normal type of Human organization.—Not only is the distinction of sexes altogether wanting at first, but the conformation of the external parts of the apparatus is originally the same in Man and the higher Mammalia as it permanently is in the Oviparous Vertebrata. For, about the fifth or sixth week of embryonic life, the opening of a *cloaca*, which is in connection with the sac of the allantois, may be seen externally, which receives the termination of the intestinal canal, the ureters, and the efferent ducts of the sexual organs; but at the tenth or eleventh week the anal aperture is separated from that of the genito-urinary canal, or 'uro-genital sinus,' by the development of a transverse band; and the uro-genital sinus itself is gradually separated by a like process of division into a 'pars urinaria' and a 'pars genitalis,' the former of which, extending towards the urachus, is converted into the urinary bladder. A partial representation of this phase of development is found in the permanent condition of the Struthious Birds and of the Implacental Mammalia. The external opening of this canal is soon observed to be bounded by two folds of skin, the rudiments of the labia majora in the female, and of the two halves of the scrotum in the male; whilst between and in front of these there is formed, as a bud from the anterior extremity of the pars genitalis, an erectile body, surmounted by a gland, and cleft or furrowed along its under surface. This body in the female is retracted into the genito-urinary canal, and becomes the clitoris, whilst the margins of its furrow are converted into the nymphæ or labia minora; and these bound the 'atrium vaginæ' or 'vestibule,' which receives the orifices of the urethra, of the vagina, and of Gaertner's canals when they are present. In the male, on the other hand, this sinus is nearly closed-in at a very early period, by the adhesion of the two folds of integument which bound it, forming that portion of the genito-urinary canal (improperly termed the 'urethra') which receives the orifices of the vesical or true urethra, of the genital sinus (vesicula prostatica), and of the vasa deferentia; the erectile body increases in prominence, and becomes the penis, whilst the margins of the furrow at its under surface unite (at about the fourteenth week), to form the anterior continuation of the contracted genito-urinary canal, which is commonly termed the spongy portion of the urethra. "In connection with the anterior and now distinct compartment of the cloaca or uro-genital sinus, and close to the junction of the latter with the base of the genital member, two glands are developed in each sex. These are the *glands of Bartholini* in the female, and those *of Cowper* in the male; opening as these glands do close to the base of the genital member, they form landmarks of first-rate importance in the determination of homologous parts of the uro-genital sinus, which

* See Prof. E. Weber's "Zusätze zur Lehre vom Baue und den Verrichtungen der Geschlechtsorgane," Leipzig, 1846; Dr. Leuckart's Art. 'Vesicula Prostatica' in "Cyclop. of Anat. and Physiol.," vol. iv.; and Prof. Watson 'On the Homologies of the Sexual Organs,' Humphry and Turner's "Journal," vol. xiv. (1879), p. 50.

differs widely in appearance in the two sexes. It will thus be found that the portion of the male uro-genital canal which intervenes between the point of entrance of the Wolffian ducts and the glands of Cowper must be homologous with that portion which in the female intervenes between the entrance of the Müllerian ducts and the glands of Bartholini. In other words, the short and wide vestibule of the human female must be homologous with the elongated and narrow lower half of the prostatic *plus* the membranous urethra in the male. Similarly, the genital members of the two sexes are strictly homologous, differing only in size. The margins of the lower or grooved surface remain apart in the female to form the vaginal bulbs, whilst in the male they coalesce to form the middle line, and complete the spongy portion of the urethra. The spongy portion of the urethra has therefore no representative in the human female. Finally, the labia majora are evidently homologous with the two halves of the scrotum."* The following Table, compiled from Banks,† Watson, and Allen Thomson,‡ gives clearly the origin and homologies of the several parts of the urino-genital system in the two sexes:—

I. COMMON BLASTEMA OF REPRODUCTIVE ORGANS.

Female.	*Embryonal.*	*Male.*
OVARY		BODY OF TESTICLE.
Furnishes the *ovigerms* and remains on the surface.	(1) Germ epithelial covering	Disappears and is replaced by serous covering of the tunica vaginalis.
Forms the *stroma* of the ovary and the Graafian follicles.	(2) Deeper blastema.	Forms glandular *seminal tubes* of testis.

II. WOLFFIAN BODIES.

Transverse tubes of *epoophoron*, or organ of Rosenmüller (parovarium).	(1) Upper tubular non-glomerular part.	*Vasa efferentia* and conivasculosi of the epididymis.
Paroophoron (Wald.)	(2) Lower glomerular part (primordial kidneys).	*Paradidymis* (Wald.) organ of Giraldès and vasa aberrantia.
Round ligament of the uterus.	(3) Ligament of the Wolffian body.	*Gubernaculum testis.*

III. WOLFFIAN DUCTS.

Tube of epoophoron.	(1) Upper and middle parts.	Convoluted tube of the *epididymis.*
Ducts of Gaertner (in cow and pig).	(2) Lower part.	*Vasa deferentia* and vesiculæ seminales.

IV. MÜLLERIAN DUCTS.

Fimbriated abdominal opening and terminal and occasional hydatids.	(1) Upper extremity.	*Hydatid of Morgagni.*
Fallopian tubes.	(2) Middle part.	Occasional tubular prolongation of the uterus masculinus.
Vagina and uterus.	(3) Lower single or median part.	Uterus masculinus (vesicula prostatica).

* Prof. Watson, loc. cit., p. 66.

† Prize Thesis, Edinburgh, 1864, "On the Wolffian Bodies of the Fœtus, and their remains in the Adult, including the Development of the Generative System."

‡ Quain's "Anat." ed. 8, vol. ii. p. 826.

External Organs.

V. SINUS URO-GENITALIS.

In the Female.	*Common Embryonal.*	*In the Male.*
Tissue uniting female urethra and vagina.	Substance surrounding genital cord.	Prostate gland, muscular and glandular tissue.
Female urethra.	Upper part of urinary pedicle	Upper portion of prostatic urethra.
Ostium vaginæ. Hymen.	Confluence of urinary and genital parts.	Verumontanum.
Vestibule.	Lower part of urinary pedicle	Lower part of prostatic and membranous urethra.
Glands of Bartholini.	Blastema.	Glands of Cowper.
Crura and corpus clitoridis.	Corpora cavernosa.	Crura and corpus penis.
Glans clitoridis and vaginal bulbs.	Corpora spongiosa.	Glans penis and corpus spongiosum urethræ.
Labia majora.	Genital ridges.	Scrotum and raphe.
Labia minora.		Cutaneous covering of the urethra.

749. In a large proportion of cases of so-called *Hermaphrodism*,* there has been either a want of completeness in the development of the Male organs, so that they present a greater or less degree of resemblance to those of the female; or the developmental process has gone on to an abnormal extent in the Female organs, so that they come to present a certain degree of resemblance to those of the male.—One of the most common malformations of the *male* organ is 'hypospadias,' or an abnormal opening of the urethra at the base of the penis, arising from incompleteness in the closure of the edges of its original furrow. But when the developmental process has been checked at an early period, the uro-genital sinus may retain more nearly its original character, and may have a wide external opening beneath the root of the penis, so as to resemble the female vagina, whilst the penis is itself destitute of any trace of the urethral canal; in some of these cases, again, the testes have not descended into the scrotum; whilst the absence of beard, the shrillness of the voice, and the fulness of the mammæ, have contributed to impart a feminine character to these individuals, their male attributes, however, being determined by the *seminiferous* character of the essential organs, the testes.†—In the *female* organs, on the other hand, a greater or less degree of resemblance to those of the male may be produced by the enlargement of the clitoris, by its furrowing or complete perforation by the urethra, by the closure of the entrance of the vagina and the cohesion of the labia, so as to present a likeness to the unfissured perineum and scrotum of the male, by the descent of the ovaries through the inguinal ring into the position of the male testes, and by the imperfect development of the uterus and mammæ; with these abnormalities are usually associated roughness of the voice and growth of hair on the chin, and a psychical character more or less virile.—*True* Hermaphrodism, in which there is an absolute combination of the essential male and female organs in the same individual, is comparatively rare. It may occur under the forms of *lateral* hermaphrodism, in which there is a genuine ovary

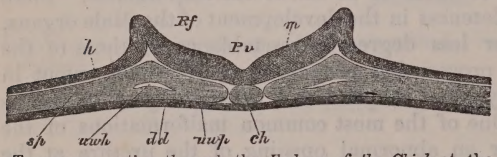
* See upon this subject, Prof. Watson, loc. cit., p. 73; Sam. Wood, "Dublin Quart. Journ. Med. Sci.," vol. xlvi. (1868), p. 52; Wieland in Fleetwood Churchill's "Practical Treatise on the Diseases of Women," 2nd ed., Paris, 1874.

† The *vesicula prostatica* has presented an unusual development in some of these cases; see Prof. Weber (loc. cit.), and Prof. Theile's 'Account of a Case of Hypospadias,' in Müller's "Archiv," 1847.

on one side and a testis on the other, in which case the external organs are usually those of a hypospadic male; *transverse* hermaphrodism, in which the external and internal organs do not correspond, the former being male and the latter female, or *vice versâ*;—and *double* or *vertical* hermaphrodism, in which the proper organs characteristic of one sex have existed, with the addition of some of those of the other; this is the rarest of all, and it is not certain that the coexistence of testes and ovaria on the same side has ever been observed in the Human species.*

750. We have now to follow the course of the development of the principal organs of *Animal* life; and shall first notice that of the *Skeleton*.† The first differentiation of parts that occurs in the mesoblast of the blastodermic vesicle (Fig. 356), is the formation of a solid cartilaginous rod, termed the notochord or chorda dorsalis (*ch*) which extends throughout the whole length of the future vertebral column, and along the base of the cranium as far as the space between the auditory capsules, or even to that point which subsequently becomes the pituitary fossa. The origin of the Notochord is still a subject of doubt; according to Kölliker‡ it is developed in Rabbits, and also in Birds from the mesoblast, appearing at first near the head, and then growing backwards at the expense of the middle layer. This is the generally received theory upon the subject. Balfour,§ however, tracing out the development of the Elasmobranchs, finds that this structure is developed originally from the hypoblast, and that it only secondarily becomes mesoblastic. This view is also supported by certain observations of Hensen‖ in regard to the development of Mammalia, whilst the drawings of Kölliker¶ seem also to lend support to the theory. Mihalkovics** is inclined to refer the origin of the notochord in all animals to the epiblast, since he believes it to be an epithelial product. The chorda dorsalis is originally composed of nucleated cells, that in the first instance lie in contact with one another, but are soon separated by the development of intercellular substance or matrix, the whole being enclosed by a delicate sheath. The chorda dorsalis, though permanent in the lowest Fishes, is only a transitory structure in Man and all the higher Vertebrata. Soon after the laying down of this cartilaginous rod, the portion of the mesoblast which immediately surrounds it (*uwp*, Fig. 356, *uw*, Fig. 357) becomes detached; and in the portion so separated the first rudiments of the vertebræ appear in the form of cubical masses on each side of the chorda dorsalis. The vertebræ appear at first as two masses of mesoblast, forming the vertebral plates, which run without interruption along each side of the notochord. Very soon, however,

FIG. 356.



Transverse section through the *Embryo of the Chick* at the close of the first day of incubation, magnified about 100 diameters:—*ch*, chorda dorsalis; *h*, epiblast, *m*, medullary portion of serous layer, *Pv*, medullary groove between the dorsal laminæ or medullary folds, *Rf* and *m*; *dd*, hypoblast; *uwp*, vertebral plate, in which the primary or protovertebræ are formed, and which is continuous with the mesoblast, *sp*; *uwh*, cleavage of the mesoblast, presenting the first indication of the pleuro-peritoneal cavity, and of the subsequent division of the mesoblast into two layers.

* On this subject, see Prof. Simpson's Article 'Hermaphrodism' in the "Cyclop. of Anat. and Phys.," vol. ii.

† See Balfour, "Studies from the Physiol. Lab. of Cambridge," Part I.

‡ "Entwickelungsgeschichte," 1879, 2nd ed., pp. 271–278.

§ Humphry and Turner's "Journal," vol. x. p. 685.

‖ "Zeitsch. f. Anat. u. Entwickelungsgeschichte," vol. i. p. 366; Lieberkühn, "Sitz. der Gesell. zu Marburg," Jan. 1876; and Kölliker, loc. cit., are opposed to these views of Hensen.

¶ Op. cit., figs. 189, 190.

** "Arch. f. Mikros. Anat.," xi. p. 389 *et seq.*

the vertebral plates are broken up by transverse lines which appear at short intervals and divide them into the quadrilateral masses known as the proto-vertebræ from which are developed, not only the permanent vertebræ, but also the episkeletal muscles. The first pair of proto-vertebræ to appear in the chick correspond with the third or fourth pair of cervical vertebræ in the adult. More externally, the mesoblast, passing outwards and downwards, and forming what is known as the Ventral Lamina, subdivides into two by a split or fissure (Fig. 357, *sp*), which is the first indication of the the pleuro-peritoneal cavity, the external or parietal layer (*hpl*) joining with the epiblast to form the *somatopleure* or walls of the abdomen with their contained structures, and ultimately meeting on the median line and enclosing the abdominal cavity in the same way that the dorsal laminæ enclose the spinal cord. The inner layer unites with the hypoblast (*df*), and forms the *splanchnopleure*, and developes the muscular and fibrous layers of the intestinal canal, the innermost layer or hypoblast (*dd*) producing the proper epithelium of the ducts and portions of the parenchyma of the several glands connected with the intestine. At this period the primitive aortæ (*ao*) and the first urinary organs or Wolffian bodies (*uwh*) begin to be formed. These, as just stated, are developed in the tissue situated externally to the chorda dorsalis, constituting a portion of the mesoblast (*uw*, Fig. 357), which now becomes separate and distinct from the remainder. The cubical masses of cells which form the original proto-vertebræ split longitudinally to form the muscle plates, and an inner portion which gives origin to the vertebral column. Soon after this period these inner portions of mesoblast (*uw*) extend themselves so as to embrace the chorda dorsalis below and the spinal cord above; the part where the two sides unite above being called by Rathke the *membrana reuniens superior*, or membranous vertebral arch. A portion of the proto-vertebræ also insinuates itself between the chorda dorsalis and the spinal cord, so that the former is entirely invested by it, and a complete vertebral column is formed, though still only *membranous*, presenting two tubes, the one posterior, formed by the arches, and enclosing the spinal cord, the other anterior, investing the chorda dorsalis. The membranous vertebral column then undergoes a process of secondary segmentation.* The transparent lines, indicating the limits of the proto-vertebræ, disappear, so that the whole vertebral column becomes fused into a homogenous mass, whose division into vertebræ is only indicated by the series of ganglia. This fusion, which does not extend to the muscle plates, is quickly followed by a fresh segmentation, the resulting segments being the rudiments of the permanent vertebræ. The new segmentation, however, does not follow the lines of the earlier division, but passes between the ganglionic and the vertebral portions, in fact through the middle of each proto-vertebra. In consequence, each spinal ganglion and nerve is attached to the hind part of the permanent ver-

FIG. 357.

Transverse section made through the *Embryo of a Fowl* at the thirty-sixth hour of incubation × 100:—*ch*, chorda dorsalis; *h*, epiblast; *mr*, medullary tube (spinal cord); *dd*, hypoblast; *uw*, proto-vertebra or better mesoblastic somite; *uwh*, transparent spherical cells occupying the centre of the same; *sp*, split in the mesoblast, dividing it into an external or fibrous layer, and an internal or serous layer, *df*, which are connected by a median lamina, *mp*. The position of the Wolffian bodies is represented by *ung*, and of the primitive aorta by *ao*.

* Foster and Balfour, "Elements of Embryology," pp. 153, 154.

tebra, immediately preceding. Similarly, the rudiment of each vertebral arch covering in the axial tube, no longer springs from the hinder part of the proto-vertebra from which it is an outgrowth, but forms the front part of the permanent vertebra to which it henceforward belongs. Each permanent vertebra is therefore formed out of portions of two consecutive proto-vertebræ. At the time when the fusion takes place, the mesoblast, which, in the form of processes from the proto-vertebral bodies, surrounds and invests the notochord, has not only increased in mass, but has also become cartilaginous; so that, as Gegenbaur points out, there is in the chick for a short period on the fifth day a continuous and unsegmented investment of the notochord. In the mammalian embryo it commences about the 6th or 7th week of fœtal life, and rapidly extends over the bodies of the future vertebræ, so that already in the 8th week a complete cartilaginous column with the membranous intervertebral ligament is formed; the chorda dorsalis now becomes attenuated and begins to disappear in the bodies of the vertebræ (Fig. 358), whereas it still remains distinct in the Ligamenta intervertebralia, and consequently presents a moniliform appearance. The formation of cartilage takes place much more slowly in the vertebral arches, not being more advanced at the 8th week than is shown in Fig. 359; so that at this period the medulla spinalis and its ganglia are only covered by the membrana reuniens superior. The arches first meet and enclose the medulla in the dorsal region; in the 4th month this is completed throughout the column, and, except in the coccygeal region, where no arches are developed, the form of the future vertebræ, in which ossification has already commenced, is perfect. The development of the atlas is irregular, its body, which is originally traversed by the chorda dorsalis, as shown by Rathke and Robin, becoming connected, not with its proper arch, but with the body of the axis forming the odontoid process of this vertebra. The ossification of the vertebræ begins at the end of the 2nd or the beginning of the 3rd month, with three centres for each vertebra, one for the body and one for the arch on each side. These parts, however, do not unite till the second year after birth. Accessory centres of ossification are subsequently formed at the tips of the spinous and transverse processes, and in the form of thin leaves at the upper and lower surfaces of the bodies, which resemble the epiphyses of the long bones. The cartilages of the *ribs* do not develop at once in their whole length, but gradually from the spine towards the sternum. Their ossification proceeds contemporaneously with those of the vertebræ from one centre for each rib, the anterior extremities of the upper seven uniting together to form a broad cartilaginous band, which constitutes one lateral half of the *sternum*, the two halves subsequently uniting from above downwards.

Fig. 358.

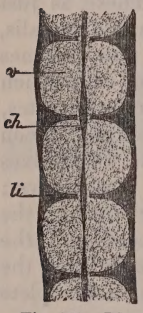


Fig. 359.

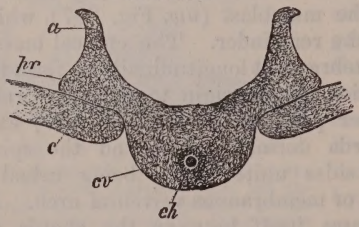


Fig. 358.—Diagram showing the attenuation of the *Chorda Dorsalis* in the middle of the bodies of the vertebræ whilst preserving its original diameter in the intervertebral spaces:—*ch*, chorda dorsalis; *v*, body of vertebra; *li*, intervertebral substance.

Fig. 359.—Diagram showing the position of the chorda dorsalis in the body of the vertebra and the formation of the neural arches:—*ch*, chorda dorsalis; *cv*, body of the vertebra; *a*, neural arch or neurapophysis; *c*, rib; *pr*, transverse process.

The morphological relations of the several parts constituting the shoulder girdle in man appear, according to the investigations of Mr. Parker,* to be as follows. Beginning with the scapula, the thin epiphysial ossification running along the vertebral border is the supra-scapular bone, well shown as segmented from the scapula in the ray and sturgeon, and large, but not quite segmented off from the scapula proper in the frogs. The whole infra-spinous portion of the bone represents the scapula proper, forming the greater portion of the scapula of the bird, but best differentiated as a distinct bone in the iguana and turtle. The acromion process, with the whole of the spinous process, constitutes the meso-scapula, which is seen partly segmented from the body of the scapula in the pangolins, but is well shown also in the iguana. The neck of the bone and the articular facet forming the glenoid region have a separate internal ossification in the frog and toad. The coracoid process forms a large separate bone in the ovipara, and in monotremes, of which only the part corresponding to the head is developed in the human subject, which speedily coalesces with the other elements forming the scapula. The portion of bone around the coracoid notch, with the fore part of the supra-spinous fossa, is the pre-scapula. It is well seen as a distinct bar above the glenoid cavity in certain lizards, and exists as a separate bone, even in the cat. The cartilaginous extremities of the clavicle are remnants of a primary rod of cartilage developed independently of the clavicles. The outer or meso-scapular segment becomes attached to the acromion by fibrous tissue, and an imperfect synovial articulation. The inner segment divides into two, of which the outer portion becomes attached to the true clavicle, whilst the internal portion, corresponding to the omo-sternum (or so-called episternum) of frogs, becomes converted into fibro-cartilage. The clavicle itself is a parosteal bar which has grafted itself on a delicate rod of cartilage.†

751. In order to facilitate the comprehension of terms now very generally employed both in Human and Comparative Anatomy in regard to the parts of a vertebra, the following description is here appended. The complete *typical vertebra* (Fig. 360, A) essentially consists, according to Prof. Owen,‡ of the *centrum*, around which are arranged four arches enclosed by processes in connection with it—viz., superiorly, the *neural* arch, which encloses the neural axis, and is formed by a pair of 'neurapophyses' (*n*, *n*) and a neural spine (*ns*); inferiorly the *hæmal* arch, which is in like special relation with the centres of the circulation, but may be expanded around the Visceral cavity generally, and which is formed of a pair of 'hæmapophyses' (*h*, *h*) and the 'hæmal spine (*h s*) and two *lateral* arches, enclosing vascular canals, which are bounded by the 'diapophyses' (*d*, *d*) and the 'parapophyses' (*p*, *p*), and are completed by the 'pleurapophyses' (*pl*, *pl*). Of these elements, the centrum is the most constant; and next to these are the neural arches, which we find in every part of the vertebral column through which the neural axis passes, and which are enormously developed in the cranial segments, in accordance with the high development of their nervous mass. The hæmal arches are

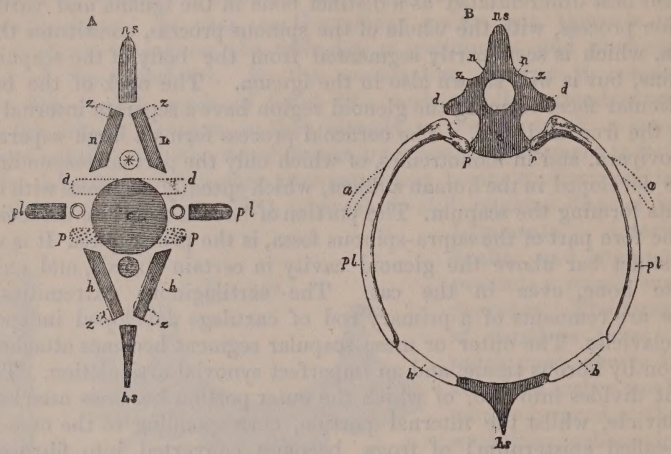
* See his important and extensive series of observations in the "Monograph on the Structure and Development of the Shoulder Girdle and Sternum in the Vertebrata," 1868, published by the Ray Society.

† Mr. Parker differentiates three kinds of ossification—"endostosis," occurring in the substance of hyaline cartilage; "ectostosis," when the bony deposit occurs in the almost structureless inner layer of the periosteum; and "parostosis," when the bone is formed in the skin, subcutaneous tissue, or in aponeuroses. Bones formed by parostosis are generally known as *membrane* or *splint* bones.

‡ See his "Archetype Skeleton," his "Lectures on Comparative Anatomy," and his "Discourse on the Nature of Limbs."

often almost entirely deficient, as in the cervical and lumbar vertebræ of Man and the Mammalia; but in the dorsal vertebræ they are very largely developed, and the elements of the lateral arches are brought into connection with them, so as to form the enclosure of the visceral cavity (Fig. 360, B). From the pleurapophyses are occasionally developed a pair of 'diverging

Fig. 360.



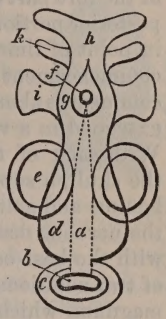
Elements of a *Vertebra* according to Prof. Owen:—A, ideal typical vertebra:—B, actual thoracic vertebra of a Bird:—*c*, centrum, giving-off *d*, *d*, the diapophyses, and *p*, *p*, the parapophyses; the neural arch, enclosing the spinal cord * is formed by *n*, *n*, the neurapophyses, and *n*, *s*, the neural spine; the hæmal arch, enclosing the great centres of the circulation, is formed by *h*, *h*, the hæmapophyses, and *h s*, the hæmal spine. From both the neurapophyses and hæmapophyses may be given-off the zygapophyses, *z*, *z*. The lateral arches, which may enclose the vertebral arteries, *o* o, are completed by the pleurapophyses, *pl*; these in B are bent downwards, so as to form part of the hæmal arch, and give-off the diverging appendages, *a*, *a*.

appendages' (*a*, *a*), which are well seen in the ribs of Birds; and these are considered by Prof. Owen to be the fundamental elements of the bones of the 'extremities' or 'limbs,' those of the anterior extremity being on his view the diverging appendages of the occipital vertebra, and those of the posterior extremity standing in the same relation to one of the sacral vertebræ. The number of the segments analogous to Vertebræ entering into the skull has been a subject of much discussion among those who adopt 'the vertebral theory' of its composition; but Prof. Owen agrees with Goethe and Oken (the original propounders of that theory) in fixing the number at *four*, which corresponds with the points of ossification, succeeding each other in a linear series, that, though absent in the earlier, are apparent in the latter stages of the development of the Encephalon, namely (proceeding from behind forwards), the Epencephalon, the Mesencephalon, the Prosencephalon, and the Rhinencephalon (Fig. 366); and also corresponding with the number of the nerves of special sense, the Auditory, Gustatory, Optic, and Olfactory, which issue from this part of the neural axis with the same segmental regularity that the ordinary sensori-motor nerves do elsewhere.

752. In the development of the *Skull* the same three stages may be traced as that in the Vertebral column—namely, the membranous, the cartilaginous, and the osseous; the result of the first two forming what is now called the Primordial Cranium. In the first stage, the membrane of the Cranium is formed of dense mesoblast from the anterior part of the proto-vertebral plates (*uwh*,

Fig. 357), which shoot forwards in front of the pointed extremity of the Chorda dorsalis or Notochord, arch upwards, and ultimately form a case for the brain.* An essential difference from those which, as we have just now seen, enclose the Spinal Cord, is however already very visible, in the perfect continuity and absence of any trace of segmentation in the basal mass. The form assumed by this deposit at a very early period is here diagrammatically shown (Fig. 361), *c* representing the atlas, or last segment of the true vertebral column, formed round the notochord, *a*, which terminates at the point *g*, where the pituitary body subsequently appears. In front of the atlas *c*, and also, like it, surrounding the notochord, a large quantity of blastema is laid down, which forms the investing mass, and to which is attached anteriorly a pair of cartilaginous rods, *g*, termed the trabeculæ cranii, that separate to enclose the pituitary fossa, and reunite in front of it to form a solid mass, the naso-frontal process which ultimately gives rise to the ali-nasal cartilages; owing to the cranial flexure, the trabeculæ at first lie in a plane different from the investing mass. From the margins of this great basal mass of the primordial cranium, a membranous investment rises up to cover the intra-cranial nervous centres. This membranous cranium, which accurately invests the rudimentary brain, is not long persistent, but soon becomes partially converted into cartilage; the change commencing at the base in the Human fœtus at least as early as the second month, whilst the upper part retains its membranous condition until a much later period. The primordial cranial axis of Man, therefore, consists of three parts—1. A membranous roof; 2. Chiefly membranous lateral walls; and 3. A cartilaginous base.

Fig. 361.



Cartilaginous basis Cranii: — *a*, chorda dorsalis; *b*, foramen magnum; *c*, atlas; *d*, lateral investing cartilaginous mass; *e*, auditory capsule; *f*, pituitary body; *g*, trabecula cranii; *h*, fronto-nasal process; *i*, alæ majores; *k*, alæ minores of the sphenoid bone.

The third, or osseous stage of development, is attained by four different processes, namely—1. By direct ossification of a portion of the cartilage of the pri-

* The various parts of the Skull, and their relations, may be understood by reference to the accompanying Diagram:—

The Primordial Skull
- i. *The investing mass*
  - The whole occipital bone → Supra-, Ex-, Basi- → -occipital.
  - The skeleton of the Ear → Peri-, Pro-, Epi-, Sphen- → -otic.
- ii. *A series of paired cartilaginous rods* attached to the investing mass by their proximal extremities, developed along the *axes of the visceral arches.*

The *First* pair of cartilaginous rods are *the Trabeculæ*
- i. The Sphenoid.
- ii. The Ethmoid.
- iii. The Nasals.

The Trabeculæ are pro-chordal (basal growths), or as has been supposed by some observers, are the remains of an anterior pair of arches.

The *First* Visceral arch is—

The Mandibular Arch
- i. Superior Maxillary process
  - i. Palatine.
  - ii. Pterygoid.
- ii. Mandibular
  - i. Meckel's cart.
    - i. Bones of the mandible.
    - ii. Articulare.
  - ii. The Quadrate

The *Second* visceral arch is—

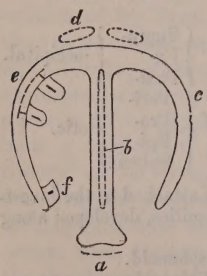
The Hyoid Arch. It consists of an azygos *basihyal* and *two ceratohyals.*

The *Third* visceral arch is—

The *First branchial* arch of Ichthyopsida. It consists of a *basi-* and *two cerato-branchials.*

mordial cranium; 2. By part of the cartilage remaining unaltered; 3. By the disappearance of a small part of the primordial cartilage; and 4. By the deposition of new bone in the form of opercular, or splint bones, on the exterior of the primordial cranium. The first point of ossification appears immediately in front of the foramen magnum about the ninth week, and is the rudiment of the basilar portion of the occipital bone; a second (sometimes double) point forms in the third month at the fore part of the Sella turcica, and is the rudiment of the basi-sphenoid, or posterior portion of the sphenoid bone. Still more anteriorly, but a little later in point of time, a third double centre of ossification may be seen, which is the commencement of the pre-sphenoid, and in front of this again an ossification commences about the middle of fœtal life, which subsequently becoming greatly extended in a vertical direction, forms the perpendicular plate of the ethmoid. With each of these centres of ossification, situated along the floor or base of the skull, a superior arch is connected, composed of bones analogous to the laminæ and spines of the vertebræ, and, like them, enclosing and protecting the nervous mass within. The formation of the superior arch in connection with the basi-occipital centre commences at an early period, by the appearance of two additional ossifying points in the cartilage on either side of the foramen magnum, which develop into the condyloid and lateral portions of the occipital bone or ex-occipitals; whilst the crown of the arch, or supra-occipital bone, represented in the adult by the broad expanded plate, is formed by two osseous points in cartilage, and one or two in the membrane immediately above the cartilage that subsequently coalesce. The upper arch of the basi-sphenoid begins as a bony deposit in the cartilage representing the great wings of the sphenoid bone, or ali-sphenoids (*i*, Fig. 361); and the crown of this arch, formed by the parietals, is exclusively produced, not by intra-cartilaginous, but by intra-membranous ossification. A third upper arch is connected with the pre-sphenoid by the ossification of the projections of the pre-sphenoid (*k*), representing the alæ minores of the sphenoid or orbito-sphenoids, the crown of this arch also, the frontal bone, developing by intra-membranous ossification, like the parietal and upper part of supra-occipital bones. The most anterior of the centres of ossification that appears in the basal cartilage of the skull, forms the lamina perpendicularis of the ethmoid (*b*, Fig. 362), and is seen in vertical section in Fig. 362. At an early period the cartilage sends out two processes, *c*, *e*, which enclose the nasal fossæ. The superior and middle turbinals (opposite *e*) are developed as outgrowths from this cartilage. The inferior turbinal (*f*) is of later date. The nasal bones, *d*, *d*, are developed as opercular bones in the membrane covering the primitive cartilage, and overlie the nasal cartilage; whilst at the base of the cartilage, but developed in membrane, is the vomer (*a*). The remaining bone which enters into the formation of the skull is the Temporal, the development of which, formerly much misunderstood, has been very carefully investigated by Prof. Huxley, Mr. Parker, and others; from whose inquiries it appears that the squamosal portion, like the parietal and frontal bones, is developed from membrane. Below this, and developed from fibrous tissue, a ring of bone appears incomplete above, forming the auditory meatus, and termed the tympanic bone. Finally, there are three centres of ossification, for which Mr. Huxley proposes the terms, *prootic*, *epiotic* and *opisthotic*. The prootic lies behind the foramen

Fig. 362.



Vertical transverse section of anterior portion of the *Primordial basis cranii*: —*a*, position of vomer; *b*, perpendicular lamina of ethmoid; *c*, right ala of the cartilage, from which the turbinal bones, *e* and *f*, are seen projecting on the opposite side; *d*, nasal bones.

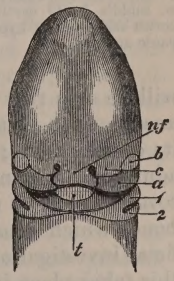
ovale, and forms the petrosal bone or petrous portion of the temporal. The epiotic surmounts the posterior vertical semicircular canal, and forms part of the mastoid portion of the temporal; whilst the opisthotic is continuous with the ossification which primitively surrounds the fenestra rotunda, and forms the floor of the Tympanum, lying in front of the point of exit of the 8th pair of nerves. The primary of the three principal sense organs, the nose, eye, and ear, are formed in connection respectively with the cerebral hemispheres, the thalamencephalon and the third primary vesicle. They are interpolated between the rudimentary parts of the head as follows:—1. The nose between the frontal, inter-maxillary and ethmoid; the eye between the frontal, sphenoid, ethmoid and maxillary; and the ear between the basi-occipital, ex-occipital, and ali-sphenoid.*

Fig. 363.

Human Embryo at the end of the third week:—1, 2, 3, 4, the visceral arches; *a*, the maxillary process; *b*, the eye.

753. The development of the *Face* next claims our attention. It proceeds from three parts, two of which are symmetrical and the third single. The former are the first pair of visceral arches (*a*, Fig. 363), sometimes termed the mandibular arch, from which the superior maxillary process is budded off on each side. The asymmetrical part is the frontal process, with its alæ or internal nasal processes (seen on each side of *nf*, Fig. 364), the development of which into the turbinals, covered by the nasals, has been already alluded to. The two lateral halves of the *first visceral arch* (1, Fig. 363) uniting in the middle line, form the rudiment of the lower jaw, and originally consist of two parts on each side, one of which, the inferior maxillary process, is cartilaginous, and becomes converted at its base into the malleus (*b*, Fig. 365), whilst its distal portion is prolonged downwards and forwards in the form of a slender rod, known under the name of Meckel's Cartilage, on the outer side of which the lower jaw (Fig. 365, *d*) is developed as a splint bone. The lower jaw thus stands in the same relation to Meckel's Cartilage that the opercular bones do to the primitive cranial bones; and it originally consists of two halves, united by a kind of synchondrosis, which does not ossify till after birth.—The malleus, which is the homologue of the quadrate bone of Birds, ossifies in the fourth month from the surface inwards, whilst Meckel's cartilage dies away, except near its root, which ossifies into the processus gracilis, or long process of the malleus. The superior maxillary process (*a*, Fig. 364) of the first visceral arch furnishes near its base the Pterygoid (*k*, Fig. 365) and distally the Palatine (*i*) bones, which begin to ossify in nascent or simple cartilage at about the close of the second month. The superior maxillary and zygomatic bones each ossify from one centre, at the end of the second month; and these, together with the lachrymals, are to be regarded as opercular bones. With regard to the inter-maxillary bone, it is probable that this is developed from two ossific centres in the membrane, independently of the superior maxilla, though they join with it about the middle of the third month.† Kollmann,‡ however, describes it as originating from the frontal process by two halves, which subsequently unite. The Vomer bears the same relation to

Fig. 364.



Human Embryo at the close of the fifth week:—1 and 2, the first two visceral arches; *a*, the superior maxillary process; *b*, the eye; *c*, the lateral naso-frontal process; *nf*, the naso-frontal process; *t*, the tongue.

* Quain's "Anat.," ed. 8, p. 732.

† See Callender, "Phil. Trans.," 1869, pt. i. pp. 163–172, plates 13 and 14.

‡ "Zeits. f. Biolog.," Band iv. 1868, p. 274.

the base of the septum nasale, it appears in the third month, and has then the form of a semi-canal. At first, the mouth is a wide cavity, which is subsequently divided into a respiratory and digestive cavity by the lateral growth of the superior maxillary processes of the first visceral arch; thus constituting partitions on either side, called Palate plates, which after the eighth week begin to coalesce from before backward. An arrest of development at this period produces the deformity termed Cleft-palate. The *second visceral or hyoid* arch is originally in connection with the base of the skull, near the posterior sphenoid bone, but subsequently becomes segmented off, its apex or proximal portion remaining as the incus and os orbiculare in Man (which represent the hyo-mandibular of Fish), whilst its distal portion is converted into the styloid process of the temporal bone and cornu minus of the hyoid with the intervening membranous part (Fig. 365, *g*, *m*, *i*). The stapes proceeds from a cartilage developed in the fenestra ovalis, and is probably a periotic element. In the third visceral arch, which corresponds with the first branchial arch of Ichthyopsida, the cornu majus of the hyoid bone is developed on each side, ossifying in the eighth month. The basal plate is a common basi-hyobranchial.

Fig. 365.

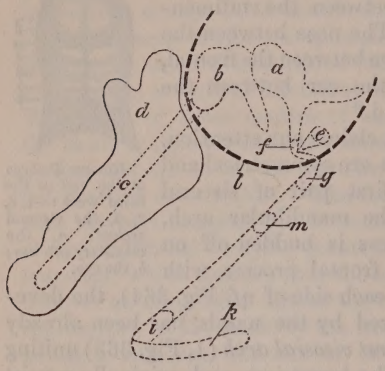


Diagram of the first and second post-oral (visceral) arches of *Human Embryo*:—*a*, incus; the line *f* points to the apex of the second arch, containing the os orbiculare; *b*, malleus; the tip of the long process is the apex of the first visceral arch; *c*, Meckel's cartilage; *d*, dentary; *e*, stapes; *f*, os orbiculare; *g*, upper hyoid cartilage; between *g* and *e* is the rudiment of the stapedius muscle; *m*, middle hyoid cartilage; *i*, rudiment of the cornu minus of os hyoides; *k*, basi-hyal; *l*, tympanic annulus.

754. From the foregoing brief outline of the development of the skull, it will be seen that no segmentation of the *cartilaginous* basis takes place at all analogous to that which occurs in the vertebral column at the same period of its development; and therefore, as Mr. Huxley observes, it is impossible to admit the existence of a series of cranial vertebræ, and still less to define their several parts by means of terms especially adapted to the description of those bones which constitute the spinal column. At the same time, a very superficial investigation of the process of ossification leads to the conclusion that this takes place in such a manner as to produce a series of segments which are the more closely analogous to those of the vertebral column the more posteriorly they are situated, as we see in the occipital and sphenoid segments; whilst in those that are more anterior, the modification of structure is so great, that scarcely any trace of the form of a vertebra remains, as appears in the case of the pre-sphenoid and ethmoidal segments.

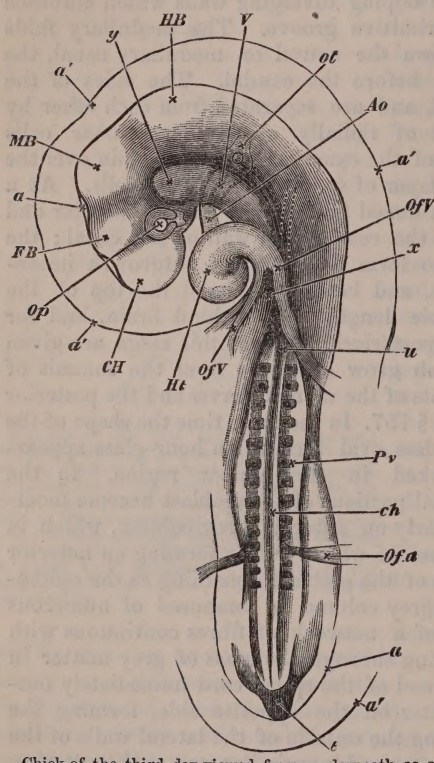
755. Within the Cranio-spinal canal thus formed, the rudiment of the Cerebro-spinal axis is found, at first under a very different aspect from that which it subsequently presents, especially as regards the relative proportion of its different segments. According to the investigations of Bidder, Kupffer, and Kölliker, in Man and Birds, the spinal cord consists, after the closure of the laminæ dorsales, of a canal surrounded by cells arranged in a radiating manner. These separate into an external layer composed of grey matter, and into an inner layer constituting the epithelium of the canal. The white substance appears later than the grey, and is unquestionably developed from it. In the first instance it consists of four cords or strands arranged in pairs,

which subsequently become connected in front by a white commissure.* According to the researches of Lockhart Clarke and Foster and Balfour, in Man, Mammalia, and Birds,† the spinal cord, in its earlier stages of development, consists of the medullary groove, which becomes narrower and deeper as it passes forwards until it reaches the head-fold, where it terminates by the medullary folds curving to meet each other and form a rounded end. Posteriorly, the medullary groove has sloping diverging walls which embrace between them the remains of the primitive groove. The medullary folds coalesce along the middle line to form the neural or medullary canal, the cervical portion of which is formed before the caudal. The sides of the neural canal are at first nearly parallel, and are separated from each other by a considerable interval, they consist of radially arranged columnar cells derived from the epiblast. The wall of the canal is exceedingly thin over the summit, where it consists of a single layer of somewhat flattened cells. At a later period the cells along the median dorsal line become slightly smaller and more spherical than those making up the rest of the wall of the canal; the spherical cells then grow upwards to form a prominent outgrowth immediately beneath the external epiblast, and between it and the top of the brain, which extends along the whole length of the hind brain, and for some distance anteriorly as well as posteriorly. From this ridge are given off at intervals paired processes which grow outwards from the summit of the cord to form the earliest rudiments of the cranial nerves and the posterior roots and ganglia of the spinal nerves.‡ § 757. In the mean time the shape of the neural canal changes from a more or less oval form to an hour-glass appearance which is more especially marked in the lumbar region. In the anterior region of the cord the external portions of the epiblast become modified into grey matter, forming anteriorly an anterior grey column, which in time is covered superficially by a mass of white matter forming an anterior white column. The internal portions of the epiblast remaining as the epithelium lining the spinal canal. The grey column is composed of numerous small nuclei which lie in the meshes of a network of fibres continuous with the fibres of the nerve root, and passing through the mass of grey matter in two directions (1) round the anterior end of the spinal cord immediately outside its epithelium, to the grey matter on the opposite side, forming the anterior commissure (2) upwards along the outside of the lateral walls of the canal. The posterior grey columns are formed in a similar way to the anterior. The walls of the constricted portion of the hour-glass shaped canal soon come into absolute contact, so that for a time two elliptical cavities are present. The roof of the posterior of these cavities is subsequently absorbed, thus transforming the canal into a wedge-shaped fissure—the posterior fissure. The anterior fissure is formed by the growth downwards of the anterior columns of the cord, which enclose between them a linear space. At a later period the posterior grey commissure and the anterior white commissure appear. As development progresses, a diversity of structure ensues in the grey substance; the cells or nuclei of the anterior grey substance becoming much larger than those of the posterior, and being connected by a coarser and more granular network. From these nuclei are developed a number of large roundish or irregular cells, with thick nucleated walls which are connected with the surrounding network, and have precisely the same appearance as the connective tissue of parts external to the cord. It appears, then, that in these early stages of development, there are at least two kinds of free

* Kölliker, "Entwick.," pp. 259, 260. † "Phil. Trans.," 1862, p. 911 *et seq.*
‡ Milnes Marshall, Humphry and Turner's "Journal," vol. xi. 1877, pp. 495, 496.

nuclei in the grey substance of the cord. One of these kinds appear to develop the general network of tissue which pervades the entire structure, but proceeds no farther; whereas each nucleus of the other kind, while connected with this network as well as with nerve-fibres, develops a nucleated cell, with a nucleated wall which is still connected, and ultimately blended, with the surrounding reticular structure. Through the medium of this intervening reticular structure, the walls of the nerve-cells, the walls of the blood-vessels, the processes of the epithelium, and the pia mater on the surface of the cord, are all uninterruptedly continuous with each other; and since the processes of nerve-cells constitute the axis-cylinders of the vaso-motor nerves distributed to parts external to the cord, Lockhart Clarke thought it probable that some of those processes which are lost by subdivision in the intervening nucleated and reticular tissue *within* the cord, were the means of transmitting nerve-power to that tissue, and through it, to the coats of its blood-vessels, from which, by their direct connection with them, the nerve-cells, in return, receive their supply of nutriment.

Fig. 366.

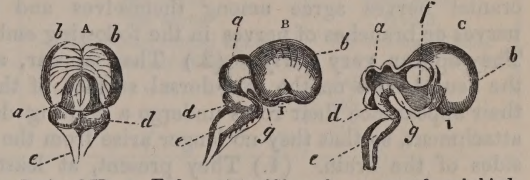


Chick of the third day viewed from underneath as a transparent object. *a'*, The outer amniotic fold or false amnion; *a*, the true amnion; *t*, tail; *CH*, cerebral hemisphere; *FB*, fore-brain or vesicle of the third ventricle; *MB*, mid-brain; *HB*, hind-brain; *op*, optic vesicle; *ot*, otic vesicle; *OfV*, omphalo-mesaraic veins forming the venous roots of the heart; *Ht*, heart, now completely twisted on itself; *Ao*, bulbus arteriosus, the thin aortic arches dimly seen uniting into the aorta, which is still more dimly seen as a curved dark line running along the body; the other curved dark line by its side ending near the reference *y* is the notochord, *ch*; *Ofa*, omphalo-mesaraic arteries; *Pv*, protovertebræ; *x*, is placed at the point of divergence of the splanchnopleure folds. The blind foregut begins here, and extends about up to *y*.

756. In the Bird, the medullary folds become closed in front, during the early part of the second day the posterior part remaining open for a short time, as the 'sinus rhomboidalis' which never completely closes in this class. The anterior extremity is dilated into a bulb, and forms the first cerebral vesicle. Two projections are formed at the sides which gradually become stalked, and constitute the optic vesicles. At the close of the second day the medullary canal presents two more dilatations separated from each other, and from the first cerebral vesicle by constrictions, so that instead of a single cerebral vesicle there are now, in addition to the optic vesicles, a series of them one behind the other. The most anterior of these, or the first cerebral vesicle, is developed into the fore-brain, the second into the mid-brain, and the third into the hind-brain. Before the end of the second day the first cerebral vesicle has begun to bud-off two small vesicles in front; these are the vesicles of the cerebral hemispheres, which subsequently become the most conspicuous part of the brain. As these are formed, owing to the more rapid growth of the upper surface of the body, the fore-brain, with the cerebral and optic vesicles, becomes slightly bent downwards over the anterior extremity

of the notochord, and this is the commencement of the cranial flexure. The cavity in the interior of each of the two vesicles of the cerebral hemispheres originating in the manner just described, constitutes the lateral ventricle, whilst the cavity of the fore-brain from which they were budded-off, remains as the cavity of the third ventricle, or, as Foster and Balfour term it, the "'tween-brain." On the summit of the 'tween-brain the rudiment of the pineal gland makes its appearance, whilst the floor is produced into the 'infundibulum,' which joins a process of the alimentary canal to form the pituitary body. The roof of the *mid-brain* becomes developed into the corpora bigemina or optic lobes in Birds, but into the corpora quadrigemina in Mammals; its floor is formed by the crura cerebri, and its cavity becomes reduced to the iter a tertio ad quartum ventriculum. In the *mid-brain* or third cerebral vesicle a constriction appears in the course of the third day, which indicates a division into the *cerebellum* in front, and the medulla oblongata behind. The fundamental parts of the brain are thus fairly mapped out in Birds on the third day. In Mammals the series of vesicles above described are distinctly visible at about the sixth week, and in the small proportion which the Cerebral Hemispheres bear to the other parts, in the absence of convolutions, in the deficiency of commissures, and in the general simplicity of structure of the whole, there is a certain correspondence between the brain of the Human embryo at this period and that of a Fish; but the resemblance is much stronger between the *fœtal* brain of the Fish and that of the Mammal; indeed, at this early period of their formation, the two could scarcely be distinguished; and it is the large amount of change which the latter undergoes, as compared with the former, that causes the wide dissimilarity of their adult forms. At about the twelfth week, we find the Cerebral Hemispheres much increased in size, and arching back over the Thalami and Corpora Quadrigemina (Fig. 367); still, however, they are destitute of convolutions, and are imperfectly connected by commissures; and there is a large cavity yet existing in the Corpora Quadrigemina, which freely communicates with the Third Ventricle. In all these particulars, there is a strong analogy between the condition of the brain of the Human embryo at this period and that of the Bird.—Up to the end of the third month, the Cerebral Hemispheres present only the rudiments of *anterior* lobes, and do not pass beyond that grade of development which is permanently characteristic of the Marsupial Mammalia, the Thalami being still but incompletely covered in by them. During the fourth and part of the fifth months, however, the middle lobes are developed from their posterior aspect, and cover the Corpora Quadrigemina; and the posterior lobes, of which there was no previous rudiment, subsequently begin to sprout from the back to the middle lobes, remaining separated from them, however, by a distinct furrow, even in the brain of the mature fœtus, and sometimes in that of older persons. In these and other particulars there is a very close correspondence between the progressive stages of development of the Human Cerebrum, and those which we encounter in the ascending series of Mammalia.*

FIG. 367.



Brain of *Human Embryo* at twelfth week:—A, seen from behind; B, side view; C, sectional view; *a*, corpora quadrigemina; *b*, *b*, hemispheres; *d*, cerebellum; *e*, medulla oblongata; *f*, optic thalamus; *g*, floor of third ventricle; I, olfactory nerve.

757. The development of the *cranial and spinal nerves* has been recently

* See an account of the observations of Prof. Retzius on the Development of the Cerebrum, in the "Archives d'Anatomie Générale et de Physiologie," 1846.

studied by Prof. Milnes Marshall,* who finds that the earliest indications of nerves in the chick occurs about the twenty-second hour in the form of a longitudinal ridge of spherical cells to which the term "*neural ridge*" has been applied (§ 755). Previous to the coalescence of the medullary folds this ridge is situated on either side of the angle of reflexion of the epiblast: at a later period it coalesces with its fellow of the opposite side, and then lies upon the top of the neural canal, forming the "*neural crest.*" It first appears opposite the widest part of the mid-brain, and gradually extends backwards and forwards. The first commencement of the individual nerves are seen as lateral outgrowths of the neural crest, which thus appears to become specially prominent at certain points. In regard to the cranial nerves, Prof. Milnes Marshall finds that the olfactory (§ 760) and third nerves are both derived from the neural crest, and he therefore believes that they are morphologically equivalent to the hinder cranial or to the spinal nerves. The auditory nerve is developed as a branch of the seventh, which in turn is derived from the neural crest. The combined seventh pair is at first continuous with its fellow across the top of the neural canal, being connected with the hind-brain at its extreme summit. This attachment is preserved, however, for only a short period, as in the later stages the nerves become connected with the sides of the brain. The sixth nerve resembles the anterior roots of the spinal nerves in arising from the sides of the neural canal, and not from the neural crest, as well as in its comparatively late appearance. The glosso-pharyngeal and vagus nerves arise as a single outgrowth on either side from the neural crest in the posterior part of the hind-brain, and behind the auditory involution. The origin of the ophthalmic fourth and fifth nerves, has not yet been accurately determined. Certain of the cranial nerves, *e.g.*, the third, the facial, and glosso-pharyngeal possess a segmental value. The mode of development of these segmental cranial nerves agree among themselves and differ sharply from other nerves or branches of nerves in the following embryological characters :—(1.) They appear very early. (2.) They appear, at least in the chick, from the neural crest on the mid-dorsal surface of the brain. (3.) Shortly after their appearance their roots undergo a shifting downward of their points of attachment, so that they no longer arise from the dorsal surface, but from the sides of the brain. (4.) They present, at least in their early stages, ganglionic enlargements on or close to their roots of origin. (5.) Their course is at right angles to the longitudinal axis of the head. (6.) Finally they have very definite relations to the segments of the head as indicated by the visceral clefts, each nerve supplying the two sides of a cleft. Of these visceral clefts, Prof. Marshall considers the olfactory as the most anterior, the olfactory being the segmental nerve in connection with it. The lachrymal or cleft in front of the maxillary arch is the second, the third nerve which divides beyond its distal ganglionic swelling being in connection with its two sides. The buccal or mouth cleft is the third visceral, it lies between the maxillary and mandibular arches, and is in connection with the fifth nerve. Behind this is the hyo-mandibular or spiracular cleft supplied by the facial nerve and constituting the fourth visceral cleft; and then the branchial clefts which are early closed, but remain in Branchiate vertebrates. The branchial clefts are seven in number, and are supplied by the glosso-pharyngeal and by the several branches of the vagus. Mr. Parker, however, does not agree with the views here adopted, chiefly on the grounds that the nasal lachrymal and oral clefts contain no hypoblast, while they are involutions and not clefts in the strict sense of the word.

* Humphry and Turner's "Journal," vol. xi. 1877, p. 490; and "Quart. Journ. Micros. Sci.," vol. xviii. 1878, p. 10; and vol. xix. 1879, p. 300.

The relations of the segmental nerves as determined by Mr. Balfour (Table A.) and Prof. Marshall (Table B) are well shown in the two following Tables:*—

Head Segments of Vertebrates.

Table A.

Segment.	Brain Vesicle.	Nerve.	Cleft.
Preoral 1	Fore-brain	i. Olfactory	Olfactory.
,, 2	Mid-brain	iii. Oculo-motor	Lachrymal.
Oral 3	Hind-brain 1st vesicle	v. Trigeminal	Buccal.
Postoral 4	Hind-brain 2nd vesicle	vii. Facial	Spiracular or hyo-mandibular.
,, 5	Hind-brain	ix. Glosso-pharyngeal	1st Branchial.
,, 6	,,	x. Vagus, 1st branch	2nd ,,
,, 7	,,	,, ,, 2nd branch	3rd ,,
,, 8	,,	,, ,, 3rd branch	4th ,,
,, 9	,,	,, ,, 4th branch	5th ,,
,, 10	,,	,, ,, 5th branch	6th ,,
,, 11	,,	,, ,, 6th branch	7th ,,

Table B.

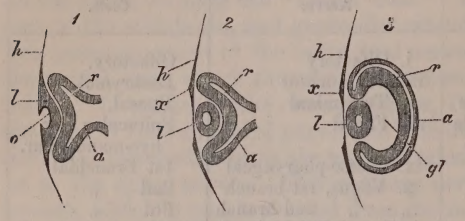
Segment.	Head Cavity.	Nerve.	Visceral Arch.
Preoral 1	1st head cavity	3rd, 4th and (?) 6th nerves (perhaps representing more than one segment)	?
Postoral 2	2nd head cavity	5th nerve	Mandibular.
,, 3	3rd ,, ,,	7th nerve	Hyoid.
,, 4	4th ,, ,,	Glosso-pharyngeal nerve	1st branchial arch.
,, 5	5th ,, ,,	1st branch of vagus	2nd ,, ,,
,, 6	6th ,, ,,	2nd ,, ,,	3rd ,, ,,
,, 7	7th ,, ,,	3rd ,, ,,	4th ,, ,,
,, 8	8th ,, ,,	4th ,, ,,	5th ,, ,,

The posterior roots and ganglia of the spinal nerves are like the cerebral nerves derived from lateral outgrowths of the neural crest, a pair of processes being given off opposite the posterior part of each proto-vertebra. The processes at first grow outwards beneath the external epiblast, but subsequently, owing to changes in the shape of the embryo, they pass downwards between the muscle-plates and the spinal cord. The proximal extremity of each process becomes more slender, and its point of attachment shifts outwards: whilst the distal portion enlarges considerably and becomes a spinal ganglion. Finally, as development proceeds, the spherical cells which form the processes become elongated and fibrillar, and somewhat resemble the cells of the mesoblast which surround them. The anterior roots of the spinal nerves appear later than the posterior roots, arising as slender outgrowths from the lower part of the sides of the spinal cord: they are composed of elongated fusiform cells, except at their points of attachment to the cord, where the cells are small and spherical The anterior roots subsequently grow out to meet the posterior, and so form the spinal nerves which run downwards on the inner side of the muscle-plate.

* Prof. Marshall, 'Morphology of the Vertebrate Olfactory Organ,' "Quart. Journ. Micros. Sci.," vol. xix. (1879), p. 334; Mr. Balfour 'Development of Elasmobranch Fishes, "Humphry and Turner's Journal," vol. xi. 1877, p. 482; "Monograph," p. 216.

758. The development of the *Eye** commences by a protrusion from the lower and posterior part of the anterior cerebral vesicle (§ 756), the cavity of the protrusion being continuous with that of the vesicle itself; very soon, however, it loses all connection with the Cerebral Hemispheres, and opens exclusively into the 'third ventricle.' As soon as the primitive optic vesicle has assumed its permanent position, the Epiblast over it becomes thickened (Fig. 368, 1), whilst the subjacent wall of the optic vesicle becomes indented, and at length so far pushed in as to form a sac composed of two layers, the edges of which surround the lens (Fig. 368, 2). This sac is the 'secondary optic vesicle' or 'cup.' The anterior thicker layer (Fig. 368, 3 *r*) is developed into the retina, the posterior (*a*) becomes the hexagonal tessellated pigment layer. The doubling-in of the primary optic vesicle is so conducted that a slit remains for a short time, termed the choroidal fissure, through which a portion of mesoblast gains entrance into the interior of the vesicle. The thickened layer of the epiblast (*e*) becoming detached constitutes the lens, a thin layer of the epiblast still remaining, which forms the epithelium of the cornea. The mesoblast surrounding the optic vesicle gradually forms a distinct investment for it, of which the outer part constitutes the sclerotic and cornea, and the inner the proper tissues and vessels of the choroid, whilst another portion penetrating more deeply constitutes the suspensory ligament and capsule of the lens, and the vitreous. The choroid only reaches as far as the edge of the lens at first, and no trace of Iris can at that time be discovered. At the end of the second month the iris, at first represented by a colourless lamina in which pigment is afterwards deposited, grows out from the edge of the choroid, and insinuates itself between the lens and the cornea. The development of the anterior half of the Retina ceases during the latter part of fœtal life, and this part is gradually transformed into the Pars ciliaris, which in the adult does not contain any nervous element. The Macula lutea is not present in the embryo, nor in the new-born infant. The optic nerve, which is at first hollow, gradually becomes solid by the growth of fibres which fill its cavity. The *Chiasma* appears at an early period, and results from the fibres of the one stalk growing over into the attachment of the other. This takes place soon after the deposition of pigment in the outer wall of the optic cup, and about the same time the fibres at the neck of the optic cup grow forward and become connected with the retina, over whose internal surface they spread.†

Fig. 368.



Longitudinal section of the *Eye of Embryo Fowl*:—1, from an embryo at about the 65th hour of incubation; 2, from an embryo a few hours older; 3, from an embryo at the 4th day of incubation:—*h*, epiblast; *l*, lens in Fig. 1, still connected with the epiblast, and possessing a small cavity (*o*) in its interior,—in Figs. 2 and 3 it is seen detached but still hollow; *r*, introverted portion of the primitive optic vesicle, subsequently becoming the retina; *a*, posterior part of the optic vesicle, which, according to Remak, probably becomes the choroid coat, ciliary processes, and iris, and in Figs. 1 and 2 is still connected with the brain by the hollow optic nerve; *x*, thickening of the epiblast around the spot from which the lens has detached itself; *gl*, vitreous body.

759. *Development of the Ear.*—The Ear makes its first appearance in the Fowl on the second day, as an involution of the Epiblast over the hind-brain;

* See the excellent Memoir of the late Mr. H. Gray in the "Philosophical Transactions," 1850; Kölliker, "Entwickel. des Menschen," 1879, pp. 623–703, et auct. ib. cit.; Peter Young, 'On the Development of the Eye in the Chick,' "Med.-Chir. Rev.," 1858, vol. xxii. p. 187; and Klebs in Virchow's "Archiv," Band xxviii.

† Foster and Balfour, "Elements of Embryology," 1874, pp. 94–111.

and the pit thus formed becomes converted into a sac by the narrowing and closure of its mouth. This sac is the 'otic vesicle,' and is lined by epiblast and surrounded by mesoblast. By the outgrowth of the vesicle in different directions, the semi-circular canals and cochlea are developed, the mesoblast forming both their membranous and osseous walls, whilst the epiblast remains as their epithelial investment, and consequently forms the proper auditory apparatus of hair cells, &c. The auditory nerve rises, as has been already stated (§ 757), in common with the facial; that portion of the combined root which becomes the auditory nerve is considerably larger than that from which the facial is derived. It passes downwards and backwards as a large ganglionic mass closely applied to the anterior wall of the auditory vesicle, with the epithelium of which it comes into contact at a very early period, and subsequently completely fuses with it. In Man the vesicles are first found about the 4th week, possessing an epithelial lining derived from the epiblast; these are the Vestibula. The vesicles or vestibules then close and become pyriform; and the small end pushes out a hollow, club-shaped process, 'processus vestibuli,' which is connected with the dura mater, its peduncle passing through the Aquæductus vestibuli to the Atrium. Dr. Urban Pritchard* finds that *the organ of Corti* is developed from a certain number of the epithelial cells lining the rudimentary ductus cochlea, which itself starts as a bud from the vestibular labyrinth. The bud elongates and assumes a spiral form, so that at an early period of development the cochlea is represented by a spiral tube lined with epithelium, and surrounded by stellate embryonic tissue. During the further development of the organ of Corti, the rods, membrana reticularis and vertical trabeculæ are formed from the walls of the original epithelial cells, whilst the ciliated and other cells are formed from their contents. The membrana tectoria is a secretion from the same original epithelium. The Semicircular Canals are at first straight tubes, receiving their characteristic curvature and ampullæ at a later period. The remaining portion of the vestibule forms the Fovea hemispherica and the Fovea hemi-elliptica. The petrous portion of the temporal bone is developed from the mesoblast surrounding the labyrinth, which subsequently becomes cartilaginous (8th week). In Man the cochlea makes one entire turn in the 8th week; at the end of the 3rd month the canal is complete. The spiral lamina is not completed till after the 6th month.—The modiolus and the spiral lamina only ossify in the last months. The Middle Ear (including the external meatus, tympanum, and Eustachian tube) is formed by the partial closure of the first branchial cleft at the 4th week. At the 3rd month the ossicula are formed, and are then seen lying *over*, not in, the tympanic cavity, imbedded in gelatinous tissue. The Eustachian tube remains closed during the whole of fœtal life by gelatinous tissue, the cartilaginous portion being formed at the 4th month. The mastoid cells only appear at puberty. The membrana tympani is at first very thick, and horizontal in position.—The *External Ear* is developed from the Annulus tympanicus, § 752, a small bone which can be separated at birth, and gradually elongates. The cartilage and auricle are formed from the skin that surrounds the outer opening of the first branchial cleft. The auditory capsule is developed, according to Huxley, from three separate ossifications arising in the periotic cartilaginous mass;—an anterior ossification, the prootic, a superior and posterior one, the epiotic, and an inferior and posterior one, the opisthotic. These ossifications unite with each other, with the squamosal and with the tympanic bone to form the temporal. Of the three

* Humphry and Turner's "Journ. of Anatomy and Physiology," vol. xiii. 1879, p. 99; "Proc. Roy. Soc.," vol. xxiv.

ossicula auditûs,* according to Prof. Parker,† the stapes is a cartilage developed in the fenestra ovalis, it is a periotic element and cannot be proved to be hyoid. It is the equivalent of the base of the columella of air-breathing ovipara. The incus is part of the hyoid arch and not of the mandibular. The mandibular is divisible into antero-superior and postero-inferior portions; the antero-superior being the pterygo-palatine. The postero-inferior part of the hyoid in Man is the styloid and cornu minus with the intervening membranous portion, the cornu majus being a rudiment of the first branchial arch of an osseous Fish. The malleus is the proximal portion of the first visceral arch, and is the modified os quadratum of fish, reptiles, &c. The processus gracilis, at an early period of fœtal life, is the cartilage of Meckel, and meets its fellow in the middle line below the mouth, forming a perfect primordial lower jaw.

760. *Organ of Smell.*—According to von Baer, the nasal fossæ are at first distinct from the oral cavity, subsequently communicate with it, and are finally divided into two portions, of which one becomes the respiratory portion of the nasal cavity, whilst the other forms the true olfactory portion and labyrinth of the Nose. In the development of the Olfactory nerve and organ,‡ the nerves arise as solid rods from the upper part or neural crest of the fore-brain before any trace of the cerebral hemispheres. With the development of the hemispheres the olfactory nerves become pushed down towards the ventral surface of the brain, and acquire a secondary connection with the hemispheres. The olfactory lobe first appears as a depression on the inner side of the fore-brain some time after the nerves are visible. The olfactory organs make their first appearance as a pair of slight thickenings of the external epiblast on the under surface of the fore-brain immediately in front of the mouth. Each thickened patch of skin soon becomes involuted as a shallow pit. Prof. Marshall points out the close analogy of the pit to a visceral cleft, and of the folds that subsequently form in it to a gill, and he concludes that the olfactory organ is the most anterior visceral cleft; that the olfactory nerve is the segmental nerve supplying the two sides of the cleft in a manner precisely similar to that in which the hinder clefts are supplied by their respective nerves; and that the Schneiderian folds are homologues of the gills. In the Human subject two depressions, the nasal fossæ, are well marked at the end of the 4th week. In the 6th week these fossæ communicate below with the oral cavity by a groove. At the end of the 2nd month the groove closes, and the labyrinth communicates with the most anterior part of the oral cavity by means of two narrow orifices, which are themselves rapidly closed by the formation of the palate dividing the nose from the mouth, slight traces of them remaining in adult life in the Naso-palatine foramen. At the 10th week the posterior nasal orifices are formed on either side of the Septum. The Labyrinth is wholly developed from the epiblast investing the nasal fossæ. It is fully formed at the close of the 3rd month, though the accessory cavities of the frontal, sphenoidal, and ethmoidal sinuses, with the antrum of Highmore, are still absent, and are not completed till after the 6th month. The outer nose begins to grow out of the nasal part of the primordial cranium about the end of the 2nd month. In the 3rd month the nasal orifices are closed by a gelatinous plug, which disappears after the 5th

* For an excellent account of the Morphology of these bones throughout the Mammalia, see an elaborate Paper by Mr. Alban Doran, "Trans. Linnean Soc.," Series ii. vol. i.

† Note to the Editor.

‡ Which has been carefully worked out by Dr. Milnes Marshall, "Quart. Journ. of Mic. Sci.," 1879, p. 300; and 1878, p. 17; and "Journ. of Anat. and Phys.," vol. xi.

month, and seems to consist of mucus and epithelial plates. The several steps of the development of this organ are met with in the various classes of animals: the small closed fossæ remind us of Fishes; the short nasal ducts opening into the anterior part of the mouth, of Batrachians, &c.

761. *The extremities* (Fig. 346, *qq*, *rr*) appear in Man about the fourth week, as small and undivided stumps from the lateral plate; those of the upper extremity appearing first: a division into two principal parts takes place in the fifth week; one of which is broad, and shows about the fifth week four indentations; the other is more cylindrical, and subdivides into a fore and upper arm about the eighth week. The two extremities are very similar in form up to this period, their distinctive characters only appearing well marked at the third month. All the bones which enter into their composition pass through stages of development similar to those that have been already described as occurring in the bones of the vertebral column and skull. In the first instance only a soft blastema or indifferent tissue appears in the place of the future bone: but this gradually develops into cartilage, the conversion being complete about the end of the second or the commencement of the third month, and in the cartilage again points of ossification make their appearance, with great though not absolute precision, for each bone, not only as regards number, but also as to time and position.* The fore and hind limbs also undergo certain changes in their position, which adapt them to their future functions.

762. *Of Sex.*—The conditions on which the differentiation of sex immediately depend are yet extremely obscure. M. Marc Thury,† who has paid great attention to this subject in cattle, has arrived at the conclusion (which, however, demands much confirmatory evidence for its establishment) that the sex of the progeny of a particular act of sexual intercourse is dependent upon the period of menstruation (in women) or of rut (in animals), at which the impregnation of the ovum takes place. If this occur at the commencement of the period, the offspring will invariably be a female; if towards the close, a male: the cause of the difference being the more advanced stage of maturation of the ovum in the latter case, owing to its having been for a longer period exposed to the warmth of the body of the mother. Ploss‡ attributes the sex of the child to the quantity and quality of the nutriment received by the mother during pregnancy, since from a review of various countries, and a comparison of the relative numbers of males and females born, he finds that when the food is abundant and plentiful, the proportion of females rises; whilst, under opposite conditions, males are most frequent. In mountainous countries the number of males also increases relatively. Preussen (loc. cit.), however, on the other hand, considers that better and more abundant food is required by the mother for the production of males; whilst other observers have supposed that the child will be of the sex of the parent who has the strongest constitution.§—There is strong statistical evidence that the relative numbers of Males and Females are in some way influenced by the relative *ages* of the parents. The following Table expresses the average results collected by M. Hofacker‖ in Germany, and by Mr. Sadler¶ in Britain; between which it will be seen that there is a very striking general correspondence, although both were drawn from a too limited series of observa-

* See Kölliker, loc. cit., ed. 2, 1879, p. 496.

† "Notice on the Law of Production of Sexes," &c., Pamphlet, 1863.

‡ Henle and Meissner, 1860, p. 210.

§ See also a Paper by Dr. Mortimer Granville, *The Lancet*, vol. ii. Oct. 1880.

‖ "Annales d'Hygiéne," Oct. 1829. ¶ "Law of Population," vol. ii. p. 343.

tions. The numbers indicate the proportion of Male births to 100 Females, under the several conditions mentioned in the first column :—

	Hofacker.		Sadler.
Father younger than Mother . . .	90·6	Father younger than Mother . . .	86·5
Father and Mother of equal age . .	90·0	Father and Mother of equal age . .	94·8
Father older by 1 to 6 years . . .	103·4	Father older by 1 to 6 years . .	103·7
„ „ 6 to 9 „ . . .	124·7	„ „ 6 to 11 „ . . .	126·7
„ „ 9 to 18 „ . . .	143·7	„ „ 11 to 16 „ . . .	147·7
„ „ 18 and more . . .	200·0	„ „ 16 and more . . .	163·2

From this it appears that the more advanced age of the Male parent has a very decided influence in occasioning a preponderance in the number of Male infants; and this tallies with the fact, that taking the average of the whole of Europe, over which (as a general rule) the state and customs of society bring about a decided preponderance of age, among married couples, on the side of the husband, the proportion is about 106 males to 100 females. This does not hold good, however, in regard to *illegitimate* offspring, the parents of which may generally be presumed to be more nearly on an equality in this respect; and it is curious that the proportion of these has averged 102·5 males to 100 females, in places where the proportion of *legitimate* births was 105¾ males to 100 females.—We are not likely to obtain data equally satisfactory in regard to the influence of more advanced age on the part of the Female parent; as a difference of 10 or 15 years on that side is not so common. If it exist to the same extent, it is probable that the same law would be found to prevail in regard to Female children born under such circumstances, as will be stated (§ 763) with respect to the Male—namely, that the mortality is greater during embryonic life and early infancy, so that the preponderance is reduced. Even at birth, there is a manifest difference in the physical conditions of infants of different sexes; for, in the average of a large number, there is a decided preponderance on the side of the Males, both as to the length and the weight of the body. And it seems not improbable that this difference has a decided influence upon the greater loss of life in the act of parturition which occurs among Male infants.

I. The *Length** of the body in fifty new-born infants of each sex showed an *average* difference of 4½ lines in favour of the Male.

II. The average Weight of infants of both sexes, as determined by Quetelet, is 3·05 kilog. or 6·77 lbs.; and this corresponds almost exactly with the statement of Chaussier, whose observations were made upon more than 20,000 infants. The mean obtained by him, without reference to distinction of sex, was 6·75 lbs.; the maximum being 11·3 lbs., and the minimum 3·2 lbs.† The average in this country is probably rather higher; according to Dr. Joseph Clarke,‡ whose inquiries were made on 60 males and 60 females, the average weight of Male children is 7⅓ lbs., and that of Females 6⅔ lbs. He adds that children which at full time weigh less than 5 lbs. rarely thrive; being generally feeble in their actions, and dying within a short time. Several instances are on record of infants whose weight at birth exceeded 15 lbs. It appears that healthy females, living in the country, and engaged in active but not over-fatiguing occupations, have generally the largest children; and this is what might be expected *à priori*, from the superior energy of their nutritive functions. A fœtus which has been full 40 weeks in utero, the

* For details of fifty cases, see Quetelet, "Sur l'Homme," tom. ii. pp. 8 and 35.

† These numbers have been erroneously stated in many Physiological works, owing to the difference between the French and English pound not having been allowed-for.

‡ "Philosophical Transactions," vol. lxxvi.

mother and father being healthy and well nourished, should measure 20 inches at birth; the *average* is 18 inches. It takes three years to grow the next 18 inches, which is four times as long as the nine months in utero, and it takes about eight years to grow the third 18 inches. After this, 2, $2\frac{1}{2}$, or 3 inches a year goes on up to the time of final retardation at puberty.*

	Ft.	In.		Ft.	In.		Ft.	In.
Birth . .	1	6	4 years . .	3	$2\frac{1}{2}$	8 years . . .	4	$0\frac{1}{2}$
1 year . .	2	4	5 „ . .	3	5	9 „ . . .	4	3
2 years . .	2	8	6 „ . .	3	$7\frac{1}{2}$	10 „ . . .	4	$5\frac{1}{2}$
3 „ . .	3	0	7 „ . .	3	10	11 „ . . .	4	8

This rate goes on up to puberty, so that at 14 the height should be 5 ft. $3\frac{1}{2}$ in. Females rarely grow much after this, but males continue to grow at the rate of 1 inch a year for 3 or 4 years, stopping at $5 \cdot 7\frac{1}{2}$. This is the rate of average English growth.

763. There appears to be, from the first, a difference in the *Viability* (or probability of life) of Male and Female children; for, out of the total number born dead, there are 3 Males to 2 Females; this proportion gradually lessens, however, during early infancy; being about 4 to 3 during the first two months, and about 4 to 5 during the next three months; after which time the deaths are nearly in proportion to the numbers of the two sexes respectively, until the age of puberty. The viability of the two sexes continues to increase during childhood; and attains its maximum between the 13th and 14th years. For a short time after this epoch has been passed, the rate of mortality is higher in Females than in Males; but from about the age of 18 to 28, the mortality is

FIG. 369.

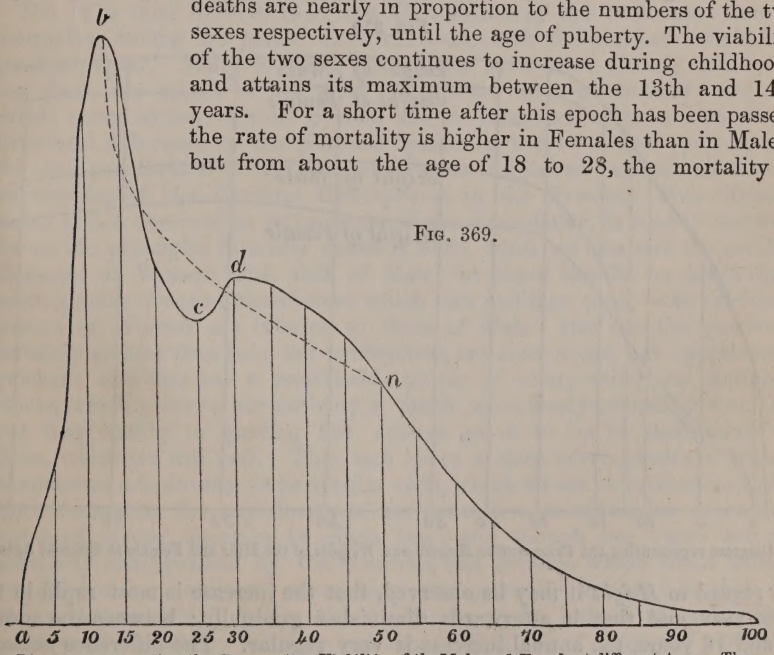


Diagram representing the *Comparative Viability of the Male and Female* at different Ages. The dotted line represents the viability of the female.

much greater in Males, being at its maximum at 25, when the viability is only half what it is at puberty. The fact is a very striking one; and shows most forcibly that the indulgence of the passions not only weakens the health, but in a great number of instances is the cause of a very premature death. From the age of 28 to that of 50, the mortality is greater and the

* 'On the Physical Development of Children,' by Percy Boulton, M.D., "The Lancet," 1880, vol. ii. p. 610.

viability less on the side of the Female; this is what would be anticipated from the increased risk to which she is liable during the parturient period. After the age of 50, the mortality is nearly the same for both.—These facts have been expressed by Quetelet* in a form which brings them prominently before the eye (Fig. 369). The relative viability of the Male at different ages is represented by a curved line; the elevation of which indicates its degree, at the respective periods marked along the base line. The dotted line, which follows a different curve, represents the viability of the Female. Starting from *a*, the period of birth, we arrive at the maximum of viability for both at *b*: from this point, the Female curve steadily descends towards *n*, at first very rapidly, but afterwards more gradually; whilst the male curve does not descend quite so soon, but afterwards falls much lower, its minimum being *c*, which corresponds with the age of 25 years. It afterwards ascends to *d*, which is the maximum of viability subsequently to the age of puberty; this point is attained at the age of 30 years, from which period, up to 50, the probability of life is greater in the Male than in the Female. In the decline of life, there seems little or no difference for the two sexes.

764. Similar diagrams have been constructed by Quetelet, to indicate the relative Heights and Weights of the two sexes at different ages (Fig 370).—

Fig. 370.

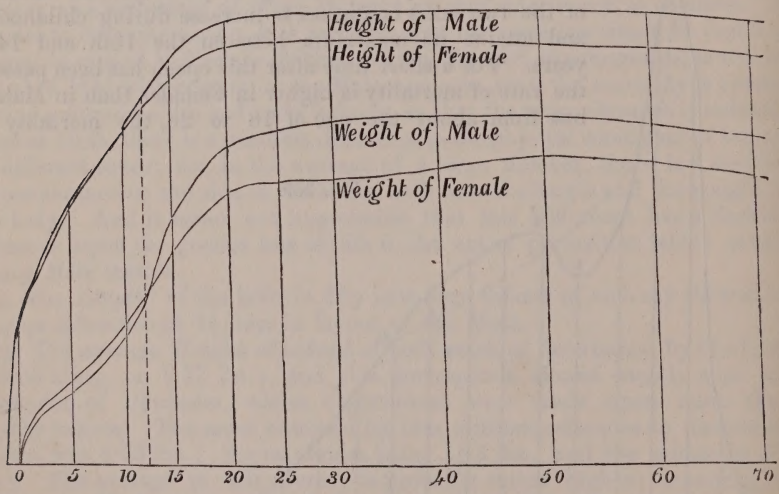


Diagram representing the *Comparative Heights and Weights* of the Male and Female at different Ages.

In regard to *Height* it may be observed, that the increase is most rapid in the first year, and that it afterwards diminishes gradually; between the ages of 5 and 16 years, the annual increase is very regular. The difference between the Height of the Male and Female, which has been already stated to present itself at birth, continues to increase during infancy and youth; it is not very decided, however, until about the 15th year, after which the growth of the Female proceeds at a much diminished rate, whilst that of the Male continues in nearly the same degree, until about the age of 19 years. It appears, then, that the Female comes to her full development in regard to Height, earlier than does the Male. It seems probable, from the observations of Quetelet, that the full Height of the Male is not generally attained until the age of

* Op. cit.

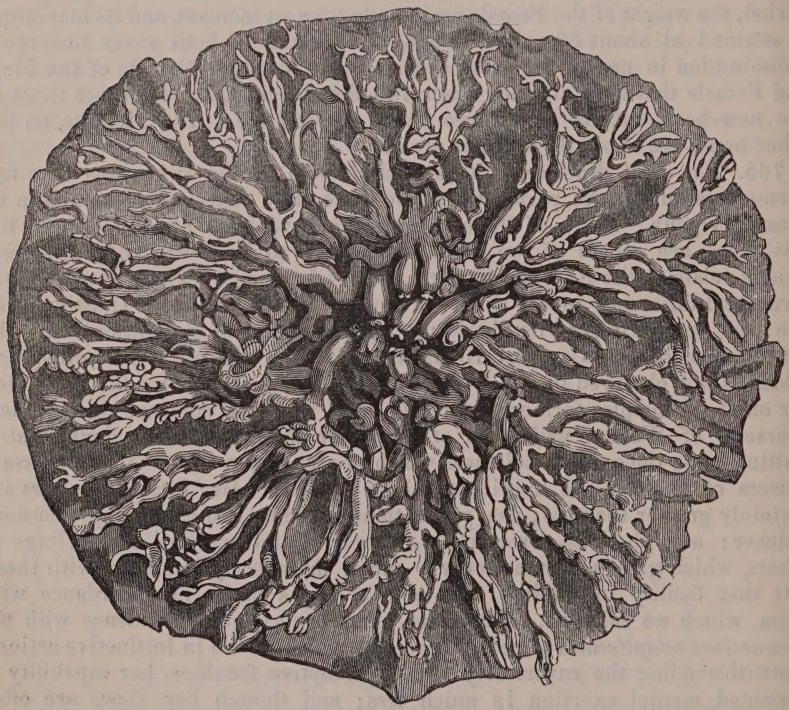
25 years. At the age of 50, both Male and Female undergo a diminution of their stature, which continues during the latter part of life.—The proportional *Weight* of the two sexes at different periods, corresponds pretty closely with their height. Starting from birth, the predominance then exhibited by the Male gradually increases during the first few years; but towards the period of puberty, the proportional weight of the Female increases; and at the age of 12 years there is no difference between the two sexes in this respect. The weight of the Male, however, then increases much more rapidly than that of the Female, especially between the ages of 15 and 20 years; after the latter period there is no considerable increase on the side of the Male, though his maximum is not attained until the age of 40; and there is an absolute diminution on the part of the Female, whose weight remains less during nearly the whole period of child-bearing. After the termination of the parturient period, the weight of the Female again undergoes an increase, and its maximum is attained at about 50. In old age, the weight of both sexes undergoes a diminution in nearly the same degree. The average Weights of the Male and Female that have attained their full development, are 20 times those of the new-born Infants of the two sexes respectively. The Heights, on the other hand, are about $3\frac{1}{4}$ times as great.*

765. The chief differences in the *Constitution* of the two sexes manifest themselves during the period when the Generative functions of each is in its greatest vigour. Many of these distinctions have been already alluded to; but there are others of too great importance to be overlooked; and these chiefly relate to the Nervous System and its functions. There is no obvious structural difference in the Nervous System of the two sexes (putting aside the local peculiarities of its distribution to the organs of generation), save the inferior size of the Cerebral Hemispheres in the Female. This difference, which is not observed in other parts of the Encephalon, is readily accounted for on the principles formerly stated (§ 506), when we compare the psychical character of Woman with that of Man; for there can be no doubt that—putting aside the exceptional cases which now and then occur—the *intellectual* powers of Woman are inferior to those of Man. Her *intuitive* powers are certainly greater than his; her perceptions are more acute, her apprehensions quicker; and she has a remarkable power of interpreting the feelings of others, which gives to her not only a much more ready sympathy with them, but that facility in guiding her actions so as to be in accordance with them, which we call *tact*. This tact bears a close correspondence with the *unconscious adaptiveness* to particular ends, which we see in Instinctive actions. Notwithstanding the superiority of her perceptive faculties, her capability of sustained mental exertion is much less; and though her views are often peculiarly distinguished by the clearness and decision which result from the strength of her intuitive sense, they are generally deficient in that comprehensiveness which brings the *whole* case to be judged of, and which is consequently necessary for their stability. With less of *volitional* power than Man possesses, she has the *emotional* in a much stronger degree. The emotions, therefore, predominate; and more frequently become the leading springs of action than they do in Man. By their direct influence upon the bodily frame they produce changes in the Organic functions, which far surpass in degree anything of the same kind that we ordinarily witness in Man; and they thus not unfrequently occasion symptoms of an anomalous kind, which are very perplexing to the Medical practitioner, though very interesting

* For an excellent Treatise on "The Stature and Bulk of Man in the British Isles," see John Beddoe, Pamphlet, 187 0, p. 191.

to the Physiological observer. But they also act as powerful motives to the Will; and, when strongly called forth, produce a degree of vigour and determination which is very surprising to those who have usually seen the individual under a different aspect. But this vigour, being due to the strong excitement of the Feelings, and not to any inherent strength of Intellect, is only sustained during the persistence of the motive, and fails as soon as this subsides. The feelings of Woman, being frequently called forth by the occurrences she witnesses around her, are naturally more disinterested than those of Man; *his* energy is more concentrated upon one object; and to this his Intellect is directed with an earnestness that too frequently either blunts his feelings, or carries them along in the same channel, thus rendering them

Fig. 371.



Distribution of the *Milk-ducts* in the Mamma of the Human Female, during lactation; the ducts injected with wax.

selfish.—In regard to the inferior development of her Intellectual powers, therefore, and to the predominance of the Instinctive, Woman must be considered as ranking below Man; but in the superior purity and elevation of her Feelings, she is as highly raised above him. Her whole character, Psychical as well as Corporeal, is beautifully adapted to supply what is deficient in Man; and to elevate and refine those powers which might otherwise be directed to low and selfish objects.

5. *Of Lactation.*

766. The new-born Infant in the Human species, as in the class of Mammalia generally, is supplied with nourishment by a secretion elaborated from the blood of its maternal parent, by certain glandular organs known as the

Mammary. The structure of these, which has been thoroughly investigated by Sir A. Cooper* and Mr. Birkett,† is extremely simple. Each gland is composed of a number of separate lobules which are connected together by connective tissue containing a few elastic fibres, in such a manner as to allow a certain degree of mobility of its parts, one upon another, which may accommodate them to the actions of the Pectoralis muscle whereon they are bound down; and the lobules are also connected by the ramifications of the lactiferous tubes, which intermingle with one another in such a manner as to destroy the simplicity and uniformity of their divisions, although they rarely inosculate. The galactophorous or terminal ducts contained in the nipple are usually about ten or twelve in number; they are straight, but of somewhat variable size; and their orifices, which are situated in the centre of the nipple, and are usually concealed by the overlapping of its sides, are narrower than the tubes themselves. At the base of the nipple, these tubes dilate into reservoirs, which extend beneath the areola and to some distance into the gland, when the breast is in a state of lactation. These are much larger in many of the lower Mammalia than in the Human female, in whom their use is to supply the immediate wants of the child when it is first applied to the breast, so that it shall not be disappointed, but shall be induced to proceed with sucking until the 'draught' be occasioned (§ 681). From each of these reservoirs commence five or six branches of the *lactiferous tubes*, each of which speedily subdivides into smaller ones; and these again divaricate, until their size is much reduced, and their extent greatly increased (Fig. 371). These, like the reservoirs and galactophorous tubes, are composed of a connective tissue sheath lined by short polyhedral or columnar epithelium cells, they differ, however, in possessing no unstriped muscular fibres; the epithelium forms a secretion of its own, which sometimes collects in considerable quantity when the milk ceases to be produced. The smaller subdivisions of the lactiferous tubes proceed to distinct lobules; so that when a branch of a galactophorous tube has been filled with injection, its attached lobules, if separated from each other by long maceration, are like a bunch of fruits clustered upon a stalk (Fig. 372). When the lactiferous tubes are pursued to their ultimate distribution, they are found to terminate in follicles, whose size, in full lactation, is that of a hole pricked in paper by the point of a very fine pin, so that, when distended with quicksilver or milk, they are just visible to the naked eye; at other times, however, the follicles do not admit of being injected, though the lactiferous tubes may have been completely filled. They consist of longer or shorter wavy and convoluted tubes possessed of cylindrical or saccular lateral branchlets. The diameter of the follicles is larger than that of the terminal ducts, each is limited by a membrana propria lined with an epithelium consisting of a single layer of granular-looking epithelium cells each with a spherical nucleus. In the centre of each follicle is a distinct lumen; in the follicles which are secreting milk the lumen is very conspicuous, and is bounded by polyhedral or cubical epithelial cells, some of

Fig. 372.

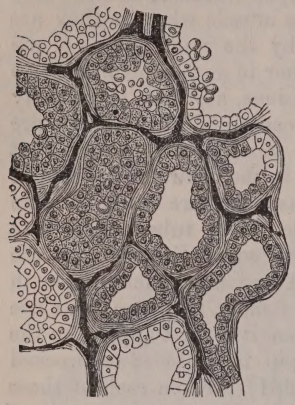
Termination of portion of *Milk-duct* in a *cluster of follicles;* from a mercurial injection; enlarged four times.

* "On the Anatomy of the Breast," 1840.

† "The Diseases of the Breast, and their Treatment," 1850. See also Giannuzzi, "Rivista Scientif. del. Akad. de Fisiocritici," ii. p. 38; Creighton, 'On the Development of the Mamma and of the Mammary Function,' Humphry and Turner's "Journal," vol. xi. 1877, p. 1; and Klein and Noble Smith's "Atlas of Histology," 1880, p. 300.

which contain larger or smaller milk globules (Fig. 373); whilst in those in which no secretion is taking place, the lumen is minute, and the epithelial cells are uniform and more or less columnar. The milk globules contained in the epithelium cells are each distinctly contained in a vacuole in the substance of the cell, but they possess their own delicate albuminous membrane. The arteries which supply the lobules with blood, become very large during lactation; and their divisions spread themselves minutely on the follicles. From the blood which they convey the milk is secreted by the epithelium and discharged into the follicles, whence it flows into the ducts. Absorbent vessels are seen to arise in large numbers in the neighbourhood of the follicles; their function appears to be to absorb the more watery part of the milk contained in the follicles and tubes, so as to render it more nutrient than it is when first secreted; and also to relieve the distension which would occur, during the absence of the child, from the continuance of the secreting process.

Fig. 373.



Section of Mammary gland.

767. The Mammary gland may be detected at an early period of fœtal existence; being easily distinguishable from the surrounding parts by the redness of its colour and its high vascularity, especially when the whole is injected. According to Dr. Creighton's observations (loc. cit.) it is first seen as a whitish strip of tissue running through a large body of fat. From the long central tract, short and inconspicuous offshoots project into the surrounding fat. The lobules develop at many separate points in this the matrix tissue, the embryonic cells from which they develop being of the same kind as those which give rise to the surrounding fat tissue. The ducts of the mamma develop from the same matrix tissue by direct aggregation of the embryonic cells along predetermined lines. In the guinea-pig, upon which these observations were conducted, the ducts develop before the lobules. The homologue of the mamma is not, therefore, a cutaneous gland of the type which is developed as an invagination of the ectoderm, but it is a fat body. At first the gland presents no difference in the male and female; and it is not until near the period of puberty that any striking change manifests itself, the gland continuing to grow, in the one sex as in the other, in proportion to the body at large. At about the age of thirteen years, however, the enlargement of the gland commences in the Female: and by sixteen, it is greatly evolved, and some of the lactiferous tubes can be injected. At about the age of twenty, the gland attains its full size previous to lactation; but the milk-follicles cannot even then be injected from the tubes. During pregnancy, the mammæ receive a greatly increased quantity of blood. This determination often commences very early, and produces a feeling of tenderness and distension, which is a valuable sign (where it exists in connection with others) of the commencement of gestation (§ 717). A true lacteal secretion* usually

* De Sinéty ("Journ. de Physiol.," July, 1875) confirms the well-known fact that the mammæ of new born infants of both sexes, especially at the third and fourth day after birth, secrete milk. The Author finds that the milk thus obtained is the result of a true secretion, and that the anatomical and physiological state of the gland is in many respects comparable to that which is to be observed during lactation in the adult female.

commences about the third or fourth month of pregnancy, and may be obtained by pressure carefully applied. This may be turned to useful account in diagnosing cases of concealed or doubtful pregnancy from cases of simple suppression of the catamenia; but it will not serve to distinguish true pregnancy from spurious, or from the distension of the uterus by tumours.* The vascularity of the gland continues to increase during pregnancy; and at the time of parturition its lobulated character can be distinctly felt. After the cessation of the catamenia from age, so that pregnancy is no longer possible, the lactiferous ducts continue open, but the milk-follicles become much reduced in size. The substance of the lobules gradually disappears, so that in old age only portions of the ducts remain, which are usually loaded with mucus; but the place of the lobules is commonly filled up by adipose tissue, so that the form of the breast is preserved. Sir A. Cooper notices a curious change, which he states to be almost invariable with age—namely, the ossification of the arteries of the breast, the large trunks as well as the branches, so that their calibre is greatly diminished or even obliterated.

768. The Mammary gland of the Male is a sort of miniature picture of that of the Female. It varies extremely in its magnitude; being in some persons of the size of a large pea; whilst in others it is an inch, or even two inches, in diameter. In its structure it corresponds exactly with that of the female, but is altogether formed on a smaller scale. It is composed of lobules containing follicles, from which ducts arise; and these follicles and ducts are not too minute to be injected, although with difficulty. The evolution of the gland goes on *pari passu* with that of the body, not undergoing an increase at any particular period; it is sometimes of considerable size in old age. A fluid, which is probably mucus, may be pressed from the nipple in many persons; and this in the dead body with even more facility than in the living. That the essential character of the gland is the same in the male as in the female is shown by the instances, of which there are now several on record, in which infants have been suckled by men (§ 748).†

769. Although the state of functional activity in the Mammary gland is usually limited to the epoch succeeding Parturition, yet this is not invariably the case; for numerous instances are on record, in which young women who

* See a valuable Paper by Dr. Peddie, 'On the Mammary Secretion,' in the "Edinb. Monthly Journal," Aug. 1848.

† The most curious fact, however, is, that even *Men* should occasionally be able to perform the duties of nurses, and should furnish an adequate supply of infantile nutriment. Several cases of this kind are upon record—see the case described by the Bishop of Cork, in the "Philosophical Transactions," vol. xli. p. 813: one mentioned by Sir John Franklin ("Narrative of a Journey to the Polar Sea," p. 157): and one which fell under the notice of the celebrated traveller Humboldt ("Personal Narrative," vol. iii. p. 58)—but one of the most recent and authentic is that given by Dr. Dunglison ("Human Physiology," 7th edit., vol. ii. p. 514.)—Dr. Dunglison also mentions that in the winter of 1849–50, an athletic man, twenty-two years of age, presented himself at the Jefferson Medical College at Philadelphia, whose left mamma, *without any assignable cause*, had become greatly developed, and secreted milk copiously.—It may be added that a lactescent fluid, apparently presenting the character of true milk, may frequently be expressed from the mammary glands of infants. (See "Dublin Medical Press," April 17, 1850.) "Professor Hall, of the University of Maryland, exhibited to his Obstetrical class, in the year 1837, a coloured man, fifty-five years of age, who had large, soft, well-formed mammæ, rather more conical than those of the female, and projecting fully seven inches from the chest; with perfect and large nipples. The glandular structure seemed to the touch to be exactly like that of the female. This man had officiated as wet-nurse for several years in the family of his mistress; and he represented that the secretion of milk was induced by applying the children entrusted to his care, to the breasts during the night. When the milk was no longer required, great difficulty was experienced in arresting the secretion. His genital organs were fully developed." Corresponding facts are also recorded of the male of several of the lower animals.

have never borne children, and even old women long past the period of child-bearing, have had such a copious flow of milk as to be able to act as efficient nurses.* In these cases, the strong desire to furnish milk, and continued irritation of the nipple by the infant's mouth, seemed to have furnished the stimulus requisite for the formation of the secretion, and it has been found that this is usually adequate to *restore* the secretion, after it has been intermitted for some months during the ordinary period of lactation, in consequence of disorder or debility on the part of the mother, or any other cause; so that where her condition renders it advisable that she should discontinue nursing for a time, the child may be withdrawn and the milk 'dried up,' with a confident expectation that the secretion may be reproduced subsequently.† Dr. M'William mentions in his Report of the Niger Expedition,‡ that the inhabitants of Bona Vista (Cape de Verde Island) are accustomed to provide a wet nurse in cases of emergency, in the person of any woman who has once borne a child and is still within the age of child-bearing, by continued fomentation of the mammæ with a decoction of the leaves of the *jatropha curcas*, and by suction of the nipple.

770. The secretion of *Milk* consists of Water holding in solution Sugar, various Saline ingredients, and the peculiar albuminous substance termed Casein; and having Oleaginous particles suspended in it. Its reaction is sometimes alkaline, sometimes neutral, and sometimes acid. Cows' milk is usually, and the milk of Carnivora always, acid,§ from the presence of free lactic acid. Human milk appears, however, to have a decidedly alkaline reaction when it is perfectly fresh; it soon, however, becomes acid. Its sp. gr. is 1032. Its index of refraction for light was found by Valentin‖ to be in different women 1·3494 on the third day after delivery, 1·3483 on the sixth day, and 1·3475 on the fifteenth day. The constitution of this fluid is made evident by the ordinary processes to which it is subjected in domestic economy. If it be allowed to stand for some time, exposed to the air, the greater part of the oleaginous globules come to the surface, being of less specific gravity than the fluid through which they are diffused: this is especially the case with the larger facetted globules, which have been hence distinguished as 'cream globules.' The *cream* thus formed does not, however, consist of oily particles alone; but includes a considerable amount of casein, with the sugar and salts of the milk. It has a sp. gr. of 1·024. These are further separated by the continued agitation of the cream; which, by rupturing the envelopes of the oil-globules separates it into *butter*, formed by their aggregation, and *buttermilk*, with a sp. gr. of 1034, containing the casein, sugar, &c. A considerable quantity of casein, however, is entangled with the oleaginous matter, and this has a tendency to decompose, so as to render the butter rancid; it may be separated by keeping the butter melted at the temperature of 180°, when the casein will fall to the bottom, leaving the butter pure and much less liable to change.—The milk, after the cream has been removed, still contains the greatest part of its casein and sugar. The amount of casein and of fat increases when milk is allowed to stand for twenty-four hours,

* A collection of such cases is given in Dr. Dunglison's "Human Physiology," 7th edit., vol. ii. p. 513.

† See an account of M. Trousseau's experience on this point, in "L'Union Médicale," 1852, No. 7; and Paper by Dr. Ballou in the "Amer. Journ. of Med. Sci.," Jan. 1852.

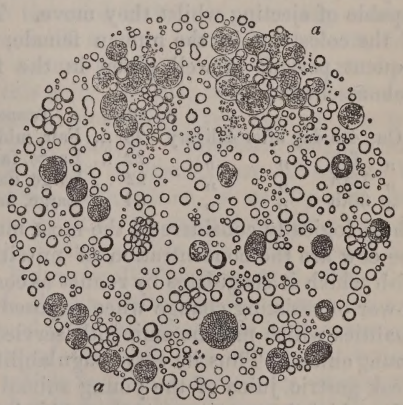
‡ "Medical Gazette," Jan. 1847.

§ v. Gorup-Besanez, p. 388. See in regard to the comparative chemistry of the cow and goat, Bogomoloff, "Centralblatt," 1871, p. 625.

‖ Pflüger's "Archiv," Band xix. 1879, p. 85.

the former at the expense of the albumin,* and the latter under the influence of fungi. Thus Kemmerich found in colostrum (§ 772), immediately after withdrawal, 31¼ parts of casein, and 43½ parts of albumin, but after the lapse of 24 hours these proportions were reversed, the quantities being 42·4 of casein and 30·6 of albumin.† If it be kept long enough, a spontaneous change takes place in its composition; the milk sugar or lactose is converted into lactic acid by a process of fermentation induced by a small particular ferment, the Bacterium lactis, and this coagulates the casein, precipitating it in small flakes.‡ Hammarsten§ believes that the presence of milk sugar is not necessary to the change, and that the ferment itself does not give rise to a lactic acid fermentation. He holds that the curdling of milk is due not to the mere precipitation of casein, but to the formation of an insoluble casein by the splitting up of a previously soluble form. The same precipitation may be accomplished at any time by the addition of an acid; all the acids, however, which act upon albumin, do not precipitate casein, as will presently be pointed out in detail. The most effectual means of effecting this is by the dried stomach of a calf, known as *rennet*. This peculiar property of curdling milk is due to the presence of a distinct ferment, and does not depend upon the acid of the gastric juice, since it takes place when the milk is neutral or faintly alkaline. Neither is it due to the pepsin of the stomach, for infusions may be prepared which have no digestive action on albumin, whilst they possess powerful milk curdling properties. The power of curdling milk is not confined to the stomach of the calf, as it exists in a greater or less degree in the stomachs of a great number of the domestic animals. A similar ferment has recently been found in the pancreas and in the succus entericus by Dr. Roberts of Manchester.‖ In the case of the pancreas the rennet ferment exists in the pig, sheep, calf, ox, and fowl, and is distinct from Trypsin. The whey left after the curd has been separated contains a large proportion of the saccharine and saline matters which entered into the original composition of the milk; this may be readily separated by evaporation.

Fig. 374.



Microscopic appearance of *Human Milk*, with an intermixture of Colostrum corpuscles at *a*, *a*, and elsewhere.

771. When Milk is examined with the Microscope, it is seen to be an emulsion, consisting of a large number of particles, of irregular size and form, suspended in a somewhat turbid fluid (Fig. 374); these particles vary in size from about the 1–12,700th to the 1–3040th of an inch; and they are termed 'milk-globules.' They are not affected by the mere contact of ether

* Kemmerich, Pflüger's "Archiv," Band ii. p. 401.

† For a Discussion on the resemblances and differences between Casein and Alkali albuminate, see Soxlet, "Journ. f. Pract. Chemie," 1872, Band vi. p. 1.

‡ See Listér on the 'Nature of Fermentation,' "Quarterly Journal of Micros. Sci.," vol. xviii. (1878), pp. 183–194.

§ "Upsala Läkareförenings Förhandlingar," Band viii. 1872, p. 63; quoted in Foster's "Text Book of Physiology," ed. 3, 1879, p. 228.

‖ The Lumleian Lectures on the 'Digestive Ferments, and the Preparation and Use of Artificially Digested Food,' the "British Med. Journ.," 1880, p. 614.

or alkalies; but if these reagents are shaken with them, an immediate solution is the result. The same effect happens if they are first treated with acetic acid. Hence it is evident that the globules consist of oily matter, enclosed in an envelope of some kind; and an extremely delicate pellicle may, in fact, be distinguished, after the removal of the oily matter by ether, or after the globules have been ruptured and their contents pressed out, by rubbing a drop of milk between two plates of glass. No proof of the organization of this pellicle has, however, been detected; and it is probably to be regarded as the simple result of the contact of oil with albuminous matter.* —Besides these milk-globules, other globules of much smaller size are seen in milk; and these present the peculiar Brownian movement which is exhibited by molecules in general. Most of them seem to consist of oily matter not enclosed in an envelope, as they are at once dissolved when the fluid is treated with ether, but, according to the statements of Donné, it would seem that a portion of them are composed of casein, suspended, not dissolved, in the fluid.

772. The *Colostrum*, or milk secreted during the first week after delivery, is of a rich yellow colour, less fluid than the milk of a later period, of a higher specific gravity (1075), strongly alkaline, and containing large oil globules, a few irregular flakes, probably epithelium scales, a little granular matter like curd, and a small number of granular corpuscles, *the colostrum corpuscles* (Fig. 374, *a a*), the largest of which are about 1–500th part of an inch in diameter, an excess of milk sugar, and very little casein. It coagulates on being heated to about 163° F.† The granular corpuscles, when maintained at a temperature of 100° F., exhibit feeble amœboid movements (Stricker and Schwartz). They are probably epithelial cells of the mammary ducts, since they are nucleated cells more or less filled with milk globules, which they are capable of ejecting whilst they move. The chemical composition of the solids of the colostrum in the human female, as compared with the milk of a subsequent period, is well given in the following percentage Table by Dr. Tolmatscheff:‡—

	Age.	Temperament.	Casein & Album.	Fat.	Sugar.
On 4th day after delivery	23 ...	Fair, middle stature	... 4·188 ...	2·471 ...	4·33
„ 6th „ „	22 ...	Large, fair, strong	... 2·050 ...	3·177 ...	5·76
„ 15th „ „	22 ...	Large, dark, strong	... 2·077 ...	2·939 ...	5·90
„ 36th „ „	34 ...	Large, fair, strong	... 1·104 ...	1·713 ...	6·26

Physiologically considered,§ the most marked peculiarities of the colostrum in the cow are the concentration of nutritive matter in it; the greater facility with which it coagulates by rennet as compared with older milk, and its greater power of resisting change when exposed to the action of air. All of these are qualities which may be eminently servicable, viewing it as the first food of the young animal. Thus its easy coagulability may be adapted to the comparatively weak gastric juice of the young animal. The excess of sugar and inorganic salts which it contains, together with its power of remaining semi-fluid, may promote the removal of the meconium by causing it to act as a laxative, whilst its concentration as nutritive matter may permit it to fulfil the same office for the young mammal as the food-yolk for the oviparous vertebrate. According to Bernard,‖ the Colostrum of the Human female contains a very large quantity of albumin, since it coagulates *en masse* when it is heated. At a later period

* The presence of an albuminous envelope to the oil globules floating in milk has been called in question by Kehrer, "Archiv f. Gynæcol.," Band ii. 1871, p. 1 (see also Zahn, Pflüger's "Archiv," 1869, p. 598), but it is maintained by Schwalbe, Max Schultze's "Archiv," Band viii. p. 269.

† See also Bernard, "Leçons," vol. ii. 1859, p. 224.

‡ Hoppe-Seyler, "Med. Chem. Unters.," 1867, p. 272.

§ "Physiological Researches," by J. Davy, M.D., F.R.S., 1863, p. 141.

‖ "Leçons," vol. ii. 1859, p. 224.

none can be discovered by this method; but if sulphate of magnesia be added, all the casein and the butter will be thrown down, and on filtration will be left on the filter with the sulphate of magnesia; the filtrate will then contain the albumins and the sugar of milk, and will coagulate on heat. All the larger globules of oil may be removed by repeated filtration; and the fluid is then nearly transparent. This, in fact, is the simplest way of separating the oleaginous from the other constituents of the milk, as but little casein then adheres to the former. The transparent fluid, which has passed through the filter, contains nearly the whole amount of the casein of the milk; but even in this fluid there are found globules too minute to be kept back by the filter, whose chemical reactions mark them as oleaginous.

773. We shall now consider the chemical characters of each of the foregoing ingredients.—The *Oleaginous* matter of milk principally consists of the ordinary components of fat—viz., palmitin, stearin, and olein; but it also contains another substance peculiar to it, designated as *butyrin*, to which the peculiar smell and taste of butter are due; this yields on saponification several volatile acids, of strong animal odour, to which Chevreul has given the names of butyric, caproic, caprylic, and capric acids. These peculiar acids are not only formed when the butyrin is treated with alkalies, but are produced by the ordinary decomposition of this principle, which is favoured by time and moderate warmth.—The *Casein** of Human milk, however, by some chemists regarded as only a combination of albumin with soda, and therefore called the Alkali Albuminate (§ 770), is usually said to be much less precipitable by acids than is that of the Cow; very commonly resisting the action of the mineral acids, and even that of the acetic (in such cases it may be thrown down by passing a current of carbonic acid gas through the acidified milk), but being always coagulated by rennet,† though the curd is long in collecting. Acetic acid without heat produces in Human milk a slow separation of soft, flaky coagula; but when heat is employed, a more perfect coagulation is produced by small than by large quantities of this acid. Gastric rennet does not seem to act upon casein if an alkali be present in more than a very minute quantity, it acts most energetically in a weakly acid solution. Pancreatic rennet curdles milk which contains as much as four grains of bicarbonate of soda to the ounce of milk: it also appears to curdle milk which is weakly acid more readily than one which has a neutral reaction.‡ In several of these particulars, as well as in its small proportional amount, the Casein of Asses' Milk bears a closer resemblance to that of Human milk than does that of the Cow. Milk also contains an albumin which closely resembles the serum albumin contained in blood; it may be obtained after the casein has been coagulated and filtered off, by exact neutralization of the milk and subsequent boiling. —Lactose, or the *Sugar of Milk*,§ which may be obtained by evaporating whey to the consistence of a syrup, and then setting it aside to crystallize, forms four-sided prisms, whose composition is $C_{12}H_{24}O_{12}$. It has a specific gravity of 1534, and a feebly sweet taste; it is insoluble in ether and absolute alcohol; slowly soluble in cold and more rapidly in boiling water. In many of its properties it bears a close resemblance to Glucose or Grape sugar, into which it is converted by the agency of dilute sulphuric or hydrochloric acid, or

* For experiments by Dr. Moore upon the casein of milk, see "Dublin Quart. Journ. of Med. Sci.," vol. vii. p. 280.

† For a detailed account of the changes which milk undergoes, see Roberts' 'Lumleian Lectures,' the "British Med. Journ.," May 1, 1880, p. 648.

‡ Roberts' 'Lumleian Lectures.' "British Medical Journal," April 24, 1880, p. 614.

§ For two simple methods of determining the quantity of sugar in milk, see Gschleidlen, "Pflüger's Archiv," Band xvi. (1878) p. 131.

by the acetic or citric acids. It is readily made to pass into the lactic and butyric fermentation by the appropriate ferments; but is with difficulty brought to undergo alcoholic fermentation.—The *Saline* matter contained in milk appears to be nearly identical with that of the blood; with a larger proportion of the phosphates of lime and magnesia, which amount to 2 or $2\frac{1}{2}$ parts in 1000. These phosphates are held in solution chiefly by the casein, which seems to have a power of combining with them even greater than that of albumin; the presence of a minute proportion of free alkali also assists their solution. A small portion of iron in the state of phosphate, together with the chlorides of potassium and sodium, and traces of potassium phosphates, magnesium phosphates, lecithin, cholesterin, alcohol, butyric, lactic and acetic acids; silicon and fluorin, odorous substances, may also be detected in milk.*

774. The proportion of these different constituents is liable to great variation from several causes. Thus, the whole amount of the solid constituents may vary from 86 to 138·6 parts in 1000; the difference being partly due to individual constitution, but in great part also to the amount and character of the ingesta. The average seems to be between 100 and 120 parts. The following Table† will serve to indicate the usual composition, as well as the ordinary variations occurring in Human milk :—

	Joly and Filhol.‡	Bödecker.	Griffith.	Becquerel and Vernois.	Simon.	Henry and Chevallier.	Brunner.§
Water	874·6	882·2	875·00	889·08	861·8—914·0	879·5	900
Sugar of Milk . .	68	64·6	61·76	43·64	39·2— 62·4	65·0	62·0
Fat	47·5	31·0	25·41	26·66	8·0— 54·0	35·5	17·3
Albumin, Casein, &c.	9·8	19·0	12·68	39·24	19·6— 45·0	15·2	6·3
Salts	1·1	3·3	1·55	1·38	1·6— 2·7	4·5	14·0

Schukowsky‖ gives 30 per 100 as the average proportion of oleaginous matters in the milk of Russian women. Milk contains about 3–7 per cent. of its volume of Gas, having a percentage composition of 55·15 of Carbonic acid, 40·56 of Nitrogen, and 4·29 of Oxygen. It further appears from the analyses of Simon, that the proportion of the different ingredients is liable to variation according to the time which has elapsed since parturition. The milk only acquires its normal characteristics some days after parturition; the colostrum corpuscles disappear within the first eight days. Milk does not retain the same composition throughout the whole period of lactation; thus the casein and butter increase up to the second month, and then diminish in quantity, the butter during the fifth month, and the casein during the tenth month; the sugar diminishes during the first month and increases from the eighth; lastly, the salts increase during the first five months and then progressively diminish. Milk which has remained in the gland is richer in fixed principles, and the last portions withdrawn are always richer in butter and casein, though the quantity of milk and the proportion of butter which it contains increase. Evening milk is said to be richer in solids, and to contain twice the amount of butter, and rather more casein than the morning milk.¶ —That some of the variations, moreover, are due to the character of the ingesta, and others to the external temperature, amount of exercise, and other circumstances affecting the individual, is proved by the inquiries of Dr. Playfair upon the Milk of the Cow. He has shown that the amount of butter

* Haidlen in "Annalen der Chemie und Pharmacie," Band xlv. p. 163.

† Canstatt's "Jahresbericht," 1860. ‡ Henle and Meissner's "Bericht," 1857, p. 329.

§ Brunner, Pflüger's "Archiv," Band vii. 1873, p. 421.

‖ Pflüger's "Archiv," 1874, Band viii. p. 597. See also Lowit for a comparison of the results obtained by analysing milk in the several ways recommended by Trommer, Hoppe-Seyler, and Schukowsky in Pflüger's "Archiv," (1874), Band ix. p. 65.

¶ Beaunis, "Nouv. Element. de Physiol. hum.," 1876, p. 141.

depends in part upon the quantity of oily matter in the food, and in part upon the amount of exercise which the animal takes and the warmth of the atmosphere in which it is kept: exercise and cold, by increasing the respiration, eliminate part of the oily matter in the form of carbonic acid and water; whilst rest and warmth, by diminishing this drain, favour its passage into the milk. The proportion of Casein, on the other hand, is increased by exercise. Dr. Playfair's experience on this head seems to correspond with the results of common observation in Switzerland; for where the cattle pasture in very exposed situations, and are obliged to use a great deal of muscular exertion, the quantity of butter yielded by them is very small, whilst the cheese is in unusually large proportion; but these same cattle, when stall-fed, give a large quantity of butter and very little cheese. It is quite possible, moreover, that particular breeds of cattle may yield milk of a richer quality than others. Thus, Vernois and Becquerel* found that Tyrolese, Dutch and Swiss cows gave milk containing from 7 to nearly 10 per cent. of butter, with much casein and albumin; whilst the cows in the immediate neighbourhood of Paris furnished a poor "green" or "beast" milk, containing only 3·6 or 3·7 per cent. of butter and but little casein. The total amount of solid matter in the milk diminishes with age, being most abundant in nursing women of from 15 to 20 years, and smallest in those of from 35 to 40 years of age. From 20–30 there is a decrease in the amount of casein and an increase in the sugar contained in the milk; the butter is present to the greatest extent from 15–20, after which it decreases.

775. The change which naturally takes place from the condition of Colostrum to that of true Milk, during the first week of lactation, is a very important one. The Colostrum, as already stated (§ 772), has a purgative effect upon the child, which is very useful in clearing its bowels of the meconium that loads them at birth; and thus the necessity of any other purgative is generally superseded. Occasionally, however, the *colostric* character is retained by the milk during an abnormally long period; and the health of the infant is then severely affected. It is important to know that this may occur, even though the milk may present all the usual appearances of the healthy secretion; but the microscope at once detects the difference.† The return to the character of the early milk, which has been stated to take place after the expiration of about twelve months, seems to indicate that Nature designs the secretion no longer to be encouraged; the mother's milk cannot then be so nutritious to the child as other food;‡ and every medical man is familiar with the injurious consequences to which she renders herself liable by unduly prolonging lactation.§ Cases are not unfrequent, however, in which the secretion continues as long as there is a demand for it; and sometimes quite independently of this. It is the habit, among some nations, to suckle the children until they are three or four years old, and to continue doing so even though another pregnancy should supervene;‖ so that the older child is only displaced by the arrival of another infant. And it seems to be

* "L'Union Médicale," ix. No. 26.

† See Donné, "Du Lait, et en particulier celui des Nourrices;" and "Brit. and For. Med. Review," vol. vi. p. 181.

‡ On the whole subject of Infant Nutrition, the Author would strongly recommend the excellent little work of Dr. A. Combe, formerly referred to.

§ One of these, which has particularly fallen under the Author's notice, is debility of the retina, sometimes proceeding to complete amaurosis; this, if treated in time, is most commonly relieved by discontinuance of lactation, generous diet, and quinine.

‖ See Erman's "Travels in Siberia" (translated by Cooley), vol. ii. p. 527; and the "Narrative of the United States' Expedition," vol. ii. p. 138.

chiefly among those who have thus forced the mammary gland into a state of unnatural and persistent activity, that the spontaneous and irrepressible flow continues after the demand for it has ceased.*

776. It is very interesting to observe that Milk contains all the classes of principles which are required for human food—the Albuminous, the Oleaginous, the Saccharine, and the Mineral; and it is the only secreted fluid in which these all exist to any considerable amount. It is, therefore, the food most perfectly adapted for the young animal; and is the only single article supplied by Nature in which such a combination exists. Our artificial combinations will be suitable to replace it, just in proportion as they imitate its character; but in none of them can we advantageously dispense with milk, under some form or other. It should be remembered that the Saline ingredients of milk, especially the phosphates of lime, magnesia, and iron, have a very important function in the nutrition of the infant, affording the material for the consolidation of its bones, and for the production of its red blood-corpuscles; and any fluid substituted for milk, which does not contain these, is deficient in essential constituents. It is very justly remarked by Dr. Rees,† that, of all the secreted fluids, Milk is most nearly allied in its composition to Blood. The proportion of the different ingredients in the Milk of different animals is subject to considerable variation: and this fact is of much practical importance in guiding our selection, when good Human milk cannot be conveniently obtained for the nourishment of an infant. The first point to be inquired into, is the quantity of solid matter contained in each kind; this may be determined either by evaporation, or by the specific gravity of the fluid. The specific gravity of Human Milk is stated by Dr. Rees (loc. cit.) to vary between 1030 and 1035; others, however, have estimated it much lower. That of the cow appears to be usually about the same; that of the cream, however, being 1024, and that of the skimmed milk about 1035. The variation will in part depend (as in the case of the urine) upon the quantity of fluid ingested, and, in part, it is probable, upon the manner in which the milk is drawn; for it is well known to milkers, that the last milk they obtain is much richer than that with which the udder is distended at the commencement. The quantity of solid matter obtainable from Cow's Milk by evaporation, seems to be usually considerably greater than that yielded by Human Milk; and there is also a considerable difference in the relative proportions of their ingredients, there being far more casein and less sugar in the milk of the Cow than in that of the Human female. The following Table exhibits the average proportions of the different ingredients in the Milk of various animals from which that fluid is commonly obtained; these proportions, however, are liable to wide variations:—

	Woman. (Simon.)	*Cow.* (Simon.)	*Goat.* (Chevallier.)	*Sheep.* (Chevallier.)	*Ass,* (Simon.)	*Mare.* (Luiscius.)
Water	890	860	868	856	907	888
Solids	110	140	132	144	95	112
Butter	25	38	33	42	12	8
Casein	35	68	40	45	16	16
Sugar and Extractives	48	30	53	50	65	88
Fixed Salts	2	6	6	7		

It appears from this, that, whilst the milks of the Cow, Goat, and Sheep have a general correspondence with each other, those of the Ass and Mare are fluids of very dissimilar character, containing a comparatively small proportion of

* See case by Dr. Green, "New York Journ. of Med. and Surg.," Sept. 1844.

† "Cyclopædia of Anatomy and Physiology," Art. 'Milk.'

casein, and still less butter, but abounding in sugar. Hence it is that they are much more disposed to ferment than other milk; indeed the sugar of Mare's milk is so abundant, that the Tartars prepare from it a spirituous liquor, to which they give the name of *koumiss*. Although no milk more nearly approaches that of the Human female, in the proportion of its ingredients, than that of the Goat, its casein forms a peculiarly dense curd, which does not suit the stomach of the infant; besides which, the milk is tainted with the peculiar odour of the animal, which is more intense if the goat be dark-coloured. The milk of the Ass, though differing in the proportion of its ingredients, seems to bear a closer approximation in properties. The milk of the Cow will usually answer very well for the food of the infant, if care be taken to dilute it properly, according to the age of the child, and to add a little sugar. Where there is an apprehension of an early failure in the supply of Milk, the Author has found it advantageous to commence feeding the Infant once a day with this mixture, soon after the first month; the number of its meals may be progressively increased, until it becomes entirely independent of its parent, without any abrupt transition: and at the same time the proportion of water and of sugar may be diminished, in accordance with the natural change which takes place in the milk of the mother during the progress of lactation (§ 772). It must not, however, be supposed that human milk can be converted into cow's milk by the mere addition of 60 per cent. of water and about 2 per cent. of sugar, for the albuminous substances of the two kinds of milk present very different reactions. Thus, human milk is not coagulated by Acetic, Hydrochloric, Sulphuric or Nitric acids, either of which immediately cause the formation of large flakes and curds in the milk of the cow. On the whole, unless children are very carefully attended to, those fed on cow's milk or other artificial substitute for mother's milk are apt to grow up with signs of defective nutrition, indicated by anæmia and rickets.

777. In the alveoli of an actively secreting mammary gland (Fig. 373) some of the lining epithelial cells may be seen to contain one or more milk globules, each of which possesses its own albuminous coat, and lies in a vacuole in the cell. Similar globules may also be observed lying freely in the lumen of the alveoli, it is therefore probable that milk is formed as a secretion by the cells of the gland, and that it does not originate from their degradation and discharge. The albuminous coating of the milk globule is casein; it is produced in the cells by changes effected in their protoplasm under the action of a special ferment, which, according to Dähnhardt,* can be extracted from the gland tissue by means of glycerin. Kemmerich† has shown that such a conversion of albumin into casein is possible, since when milk is digested for some hours at the body temperature, the casein is increased, whilst the albumin undergoes a proportional decrease. The quantity of butter existing in milk exceeds many times the amount of fat ingested, it must therefore be formed within the organism. Heintz‡ believes that a portion of the fat may be simply withdrawn from the blood, since he detected in milk, olein, stearin and palmitin. Lactose is formed directly by the gland cells, probably from the albuminous substances which are brought to them by the blood, since a considerable quantity is found in the milk of carnivora living exclusively on a flesh diet. There is reason to believe that if, whilst the process of the secretion of milk is going on, it be suddenly checked, the retention of the material in the blood, or the re-absorption of the secreted fluid, is attended with injurious con-

* "Arch. f. Ges. Physiol.," iii. (1870), p. 586. † Ibid., ii. (1869), p. 401.
‡ "Ann. d. Chemie und Pharmacie," lxxxviii. p. 300.

sequences. Thus if, when the milk is first secreted, the child be not put to the breast, an accumulation takes place, which, if not relieved, occasions great general disturbance of the system. The narrowness of the orifices of the milk-tubes obstructs the spontaneous exit of the fluid, especially in *primiparæ;* the reservoirs and ducts become loaded: further secretion is prevented; and a state of congestion of the vessels of the gland, tending to inflammation, is induced. The accompanying fever is partly due, no doubt, to the local disturbance; but in part also, there seems reason to believe, to the re-absorption of the milk into the blood; this cannot but be injurious, since, although but little altered, the constitution of milk is essentially different, especially in regard to the quantity of crystallizable matter (sugar) which it contains.—Cases of the *vicarious* secretion of milk are not numerous; and in no instance is there any proof that the elements of the fluid were pre-existent in the blood. Some of the most curious are those in which it has been poured out from a gland in the groin; but it is probable that this was in consequence of the existence of a real repetition, in that place, of the true mammary structure; this being the situation of the mammæ in many of the inferior animals, of which the homologues in man are usually undeveloped.*

778. Of the quantity of Milk ordinarily secreted by a good Nurse, it is difficult to form a correct estimate;† since the amount which can be artificially drawn, affords no criterion of that which is secreted at the time of the 'draught' (§ 681). The quantity which can be squeezed from either breast at any one time, and which, therefore, must have been contained in its tubes and reservoirs, is about two ounces. The amount secreted is greatly influenced by the mental and physical condition of the female, and also by the quantity and character of the ingesta. In regard to the influence of the mental state upon this secretion, ample details have already been given (§ 682). With respect to the physical state most favourable to the production of an abundant supply of this important fluid, it may be stated generally, that sound health, a vigorous but not plethoric constitution, regular habits, moderate but not fatiguing exercise, and an adequate but not excessive amount of nutritious food, furnish the conditions most required.

779. The influence of various Medicines upon the Milk, is another important question which has not yet been sufficiently investigated. As a general rule, it appears that most soluble saline compounds pass into the milk as into other secretions; but there are many exceptions. Common salt, the sesqui-carbonate of soda, sulphate of soda, iodine, iodide of potassium, mercury, lead, antimony, arsenic, essence of anise, absinthe, oxide of zinc, tris-nitrate of bismuth, and sesqui-oxide of iron, the crucifera generally, and many odorous substances,‡ have been readily detected in the milk; and ordinary experience shows that the Human infant is affected by many of them when they are administered to the mother; thus the influence of mercurial medicines taken by the mother, in removing from the infant a syphilitic taint possessed by both, is well known. The vegetable purgatives, especially castor-oil, senna, and colocynth, have little effect upon the milk; hence they are to be preferred to the saline aperients, when it is not desired to act upon the bowels of the child.

* For case of vicarious secretion of milk, see "Bulletino delle Scienze Mediche," April, 1839; and "Brit. and For. Med. Review," Jan. 1840.

† For an estimate by M. Guillot, founded on the comparative weight of the Infant before and after lactation, see "L'Union Médicale," 1852, No. 16. The total amount considered by Mons. Guillot to be usually drawn in the twenty-four hours, varies from 32 oz. to 64 oz. (apoth.); but his estimates are vitiated by the extraordinary frequency of the lactations observed, the infant being put to the breast from 25 to 30 times in the twenty-four hours.

‡ See Bistrow, 'On the Passage of Iron into the Milk,' Virchow's "Archiv," xlv. 98.

CHAPTER XIX.

OF THE DIFFERENT BRANCHES OF THE HUMAN FAMILY, AND THEIR MUTUAL RELATIONS.

1. *General Considerations.*

780. On taking a general survey of the Human race, it is natural, in the first place, that we should proceed to inquire into the evidence at present possessed of its antiquity, and into the physical and social conditions which prevailed in the most remote periods of which any information can be acquired; and secondly, that we should endeavour to ascertain whether the origin of the race is attributable to a single pair whose offspring have peopled the earth, or whether there may not have been a plurality of parents or of centres from which the remarkably different nations that are now in existence have sprung. The question of the remote Antiquity of Man, though long ago suggested, has only of late years, on account of the numerous facts which seem to lend support to it, awakened a lively spirit of philosophic inquiry. When our attention has been directed to it, however, it soon appears that no subject possesses a deeper interest than the relation in which Man stands to the organic world around him, both animal and vegetable: whether he was originally created with his corporeal powers, and the intellectual faculties to which they minister already developed to their highest extent, and capable of the greatest results that have been achieved in subsequent times; or whether he is not rather to be regarded as the crown and acme of a long process of development commencing with far simpler organisms, which, under the protracted operation of external agents, and in accordance with the law of *continuous descent with modification through natural selection*, whereby those animals that are the strongest and best adapted for the special conditions of life present at any time, supplant, and ultimately exterminate the less perfectly constituted, has at length culminated in a creature that even now, howsoever noble in reason and infinite in faculties, yet presents a transitory condition only to some more exalted phase of existence. The facts on which this opinion rests are of various character and weight, and a few only of the more important can here be alluded to. We have seen that in the earliest stages of the development of the embryo of the Human subject, which in this respect presents a character common to all animals, a single cell is alone discoverable; this receiving an accession of energy from the sperm-cell, and being placed under favourable conditions for the acquisition of the materials requisite for growth, soon undergoes sub-division; and in the cellular mass thus formed a differentiation of parts takes place, by which the various organs and tissues of the body are successively evolved. In the higher forms of the animal creation we have further seen that at certain transitory stages of development a close analogy exists with the permanent conditions of creatures occupying a lower position in the scale; and that, whilst throughout the whole a wonderful unity in the process is clearly discernible, each species presents certain characteristic features which are peculiar to itself. This, it is supposed, may have occurred in the history of the world. A few great types may have been originally formed, which, in the lapse of

ages, owing to the action of external agents, as light, heat, and food, and to the perpetuation of accidental varieties especially adapted to these external conditions, have gradually resulted in the infinitely varied species that now surround us.* With this extraordinary similarity in the process of development throughout the whole animal kingdom, which seems very difficult to account for upon the theory of a separate creation for each species, it cannot be a matter of surprise that close bonds of alliance should be found in the adult period of life even amongst the most dissimilar creatures. The Birds, for instance, appear to be a singularly well-defined and separate group; yet the researches of Mr. Parker† have shown that in their osseous system they possess affinities with every other class of the Vertebrata; so that, whilst presenting the closest analogies to Reptiles, and especially to the Lacertilian group, they anticipate, on the one hand, various Mammalian characters, and on the other recede, as it were, below Reptiles, retaining different Ichthyic points of structure, which are not, as a rule, found in that class. And thus it has ever been found that the more closely the structure of even the most aberrant forms of animal life has been investigated, the wider have been the affinities discovered, often explaining what was previously obscure in the structure of others, whilst at the same time the more complete has been the proof that no real isolation of a species, much less of a genus or family, exists. It is indeed probable—and this is a point on which Dr. Darwin lays great stress—that were it possible to reproduce the entire series of forms now become extinct, a regular gradation would be presented from the lowest to the highest; and hence that, as Sir Joseph Hooker has maintained,‡ we are indebted for our means of resolving plants into limitable genera and orders simply to the extinction of the forms by which they were originally connected. The reason that the intermediate links have not been discovered is owing essentially to the imperfection of the geological record. Of that great book, comparatively few leaves have as yet been deciphered; whilst even under the most favourable circumstances, and with the largest amount of information that can be obtained from this source, it is certain that the softness of the tissues of many animals will have presented an effectual obstacle to their preservation.§ It is obvious that if this mode of explanation of the production of species be extended to its utmost limits, we may reach the extreme of simplicity; for it may well be said that if a few types only are needed, these may again be reduced in number to a greater and still greater degree, until at length we arrive at that which is common to all at some stage of their existence—the

* For a full exposition of this theory, see Darwin, "On the Origin of Species by Means of Natural Selection," &c., 1859.

† See his Paper 'On the Osteology of the Gallinaceous Birds and Tinnamous,' in the "Trans. of the Zoological Society" for Nov. 25, 1862.

‡ "Introduction to the Flora of New Zealand," 1853.

§ The occurrence of a few cases where the conditions have been favourable, as in the instance of the Tellina of the Freshwater Chalk formation of Steinheim mentioned by Oscar Schmidt (in his "Descendenzlehre," 1873, p. 87) is highly suggestive in this point of view. Here the deposit from a small inland lake may be divided into about forty petrographically distinguishable layers, and throughout the whole series the varieties of Planorbis multiformis are distributed in such a manner that individual layers are characterized as successive strata by the exclusive occurrence, or by the predominance of one or more varieties which within the layer remain constant or slightly variable, but towards the limits of the next layer lead by transition to the succeeding forms. The forms diverge so greatly, and are so constant in the main zones, that in accordance with the old conchological practice they would be unreservedly claimed as species if the connecting links were not too conspicuous and the territory too circumscribed, and if the geological period—which must, however, be reckoned by thousands of years—were not considered too insignificant. Similar statements may be made in respect to the Ammonites.

single nucleated cell—a structure which comprehends the totality of the life of some animals and vegetables, and is constantly met with as the earliest stage of development of all; whilst the whole superstructure of both kingdoms may be considered to proceed from a gradual process of development and differentiation of this primary and most simple organization. It is but just to remark, however, that Prof. Owen, one of the best authorities on this subject, has advanced a different explanation of the origin of species. He states* that, "being unable to accept the volitional hypothesis, or that of impulse from within, or the selective force exerted by outward circumstances," he deems "that a minute tendency to deviate from parental type operating through periods of adequate duration is the most probable nature, or way of operation, of the secondary law, whereby species have been derived one from the other."

781. By those who embrace the developmental theory, numerous facts have been recently collected, tending in the first place to prove that Man has existed for many thousands of years upon the face of the earth; and secondly, that the more remote the period at which he can be proved to have existed, the ruder, more savage and degraded, both in a social and a structural or physical point of view, was his condition. In regard to the former point, very strong evidence has recently been obtained by the discovery of Human remains intermingled with those of extinct animals, as the Mammoth, Cave Bear, and woolly Rhinoceros, in the *breccias* of various caverns, as in those of Liége and Engis; whilst in other instances, where no bones have been discovered, perhaps in consequence of the practice of burning the dead, almost equally unexceptional evidence has been obtained from the discovery of works of art fashioned by Human hands, as in the flint implements found buried in the drift at Abbeville in Picardy and at St. Acheul near Amiens, and those found at Hoxne in Suffolk, and in Brixham Cave near Torquay.† In these instances the geological position of the remains, as well as the circumstance of their being accompanied by the bones of so many extinct animals, alike point to a remote antiquity. In particular, a very close investigation of those found at Moulin Quignon, near Abbeville, by M. Boucher de Perthes and others, has been made by Mr. Prestwich,‡ who has shown that, although some doubts may exist respecting the authenticity of the Human jawbone and some of the flint implements recently discovered there, yet that the genuineness of other flint implements cannot be doubted, and that the age of the gravel-beds in which they have been discovered is perfectly well determined as belonging to an early Quaternary or Post-pliocene period, dating before the excavation of the valley of the Somme, and consequently to a period when the physical character of the country wore a very different aspect from that which it now presents.

782. Nor can the circumstance be disregarded, that in the oldest existing monuments, as on those of Amenophis, of Horus, and of Rhameses,§ sculpture and painting, amongst the latest of the fine arts in their devolpment, had attained to so high a degree of perfection amongst the Egyptians, that the types of the Human race there depicted may still be referred to as excellent

* "Comp. Anat. and Physiol. of Vertebrates," 1860, p. 807.

† For full information respecting which, see the "Antiquity of Man," by Sir Charles Lyell, 1863.

‡ See "Phil. Transact.," 1860, p. 277; "Proc. of the Royal Society," vol. xii. 1862, p. 38; and "Quart. Journ. of the Geological Society," Nov. 1, 1863, vol. xix. p. 497.

§ See Samuel Morton, "Crania Ægyptiaca," Philad., 1844; and the works of Champollion and Rosellini; Paul Broca, 'On the Phenomena of Hybridity in Man,' "Journal de la Physiol.," vol. iii. 1861.

portraitures of some of the still existing varieties—the Jew, the Mongol, and the Ethiopian being readily distinguishable. For this indicates, on the one hand, the wonderful permanence of particular types, and so far constitutes an argument against the Specific Unity of Man on the assumption that his duration upon the earth has not exceeded, as ordinarily computed, some 6,000 years; whilst if we estimate the period occupied in the progress to a high degree of civilization in these old times by the rate at which it has advanced in the history of modern European nations, we find it requisite to admit the lapse of a much longer period than is usually allowed, and of a long sequence of antecedent generations. In all the nations of Western Europe, in France, in England, in Germany alike, it has taken many centuries to rear the modern fabric of civilization; and the ultimate results obtained by ancient nations, however imperfectly they may be known to us, do not appear to be of so extraordinary a nature as to lead us to attribute to them a superior, if even an equal, measure of intellectual endowments with ourselves, nor on that account to admit that their progress in mental culture may have been more rapid.*

783. The evidence tending to show that the most ancient races of Man possessed a materially lower type of organization than those at present in existence, is not by any means sufficient to enable any general conclusions to be drawn respecting the truth of the developmental theory, or to show that there have been transitional links between the higher Apes and Man. In the most remarkable cranium yet discovered, that of the Neanderthal, which has been most carefully examined by Prof. Huxley, the forehead is indeed unusually low and retreating, the supra-orbital ridges prominent, and the bones remarkably thick. Yet its cubic capacity does not appear to be materially less than that of many crania that might be selected from modern nations; and hence, as Mr. Huxley adds, the first traces of the primordial stock whence Man has proceeded need no longer be sought by those who entertain any form of the doctrine of progressive development in the newest tertiaries, but must be looked for in an epoch more distant from the age of the Elephas primigenius (mammals) than that is from us.

784. Many interesting facts have recently come to light, which, whilst furnishing corroborative geological evidence of the antiquity of Man, afford important means of estimating the material and social conditions of his existence in these distant epochs. The most interesting evidence upon these points is derived from the Danish Peat Mosses. These, which are of considerable depth, varying from 30 to 40 feet or more, have been the result of the slow formation of ages; and from the extraordinary preservative power which they possess, have become the receptacles or depositaries of a series of objects, from which, by a process of inductive reasoning, the most valuable conclusions can be drawn. On the surface of the soil of Denmark at the present time there flourish magnificent forests of Beech trees, numerous trunks of which are found in the superficial layers of the Peat, mingled with those of other trees, as the Alder, the Aspen, and the Birch. With these are found various instruments constructed of iron, a metal requiring a considerable amount of technical skill in its extraction, partly on account of the chemical processes to which the ores have to be subjected, and partly on account of the extremely high temperature required for its fusion or welding. These tools are accompanied by the skulls of men presenting close analogies to the present Scandinavian type, of whom, indeed, they may be considered as the early ancestors.† Below the Beeches, the trunks of Oaks are found, and iron instruments cease to appear, being

* Sir Charles Lyell, "Antiquity of Man," p. 89.

† See also Rollestonand Greenwell "On British Barrows."

replaced by those of bronze. Sir John Lubbock* has adduced various considerations to show that these workers in bronze, which is composed of copper and tin, were of Eastern origin, and were perhaps allied to the modern Hindoo, with whom they agreed in the form of the head, in the practice of burning the dead, in their leading a pastoral and agricultural life, as evidenced by the associated remains of sheep, oxen, and pigs, and in using cylindrical as well as cubic dice. Still lower in the Peat the scene once more changes; the trunks of Pines now abound, and with these have been discovered crania belonging to a wholly different race—a race who were ignorant of even the simplest processes of metallurgy, and were only able to fashion, though often with great skill and ingenuity, a series of stone or flint instruments—hammer, chisel, saw, adze or dagger—and who were probably a hunting and fishing nation, burying their dead in tumuli or barrows. Additional information has been gained respecting this race, or the races, coeval with them, by the investigation of the Swiss Lake Habitations, the piles supporting which have been found in the lakes of Zurich, Constance, and Geneva; and still more by careful examination of the Danish "Kitchen-middings." In the former the same succession of Iron, Bronze, and Stone eras appear to have succeeded one another; whilst the latter seem to be refuse-heaps, composed of oysters, cockles, muscles, periwinkles, and other mollusca which have been thrown out around their habitations by men of the Stone period. The crania of this race are small and round, with overhanging eyebrows. The remains of dogs and various wild animals are found in the middings, which, with the canoes, and the bones of deep-sea fish, as the cod and herring, seem to show that this ancient people lived by hunting and fishing.

785. In pursuing the second branch of our inquiry, it is apparent that amongst the various tribes of Men which people the surface of the globe, and which are separated from all other animals by the characters formerly described (Chap. II.), there are differences of a very striking and important nature. They are distinguishable from each other, not only by their language, dress, manners, and customs, religious belief, and other acquired peculiarities, but by the physical conformation of their bodies; and the difference lies not merely in the colour of the skin, the nature of the hair, the form of the soft parts (such as the nose, lips, &c.), but in the shape of the skull and of other parts of the bony skeleton, which might be supposed to be less liable to variation. Now it is clearly a question of great scientific interest, as well as one that considerably affects the mode in which we regard the races that differ from our own, whether they are all of *one species*—that is, descended from the *same* or from *similar* parentage—or whether they are to be considered as *distinct species*, the first parent of the several races having had the same differences among themselves as those which are now exhibited by their descendants.

786. In order to arrive at a just conclusion on this subject, it is necessary to take a very extensive survey of the evidence furnished by a number of different lines of inquiry. Thus, in the First place, it is right to investigate what are the discriminating structural marks by which *species* are distinguished among other tribes of animals.—Secondly, it should be ascertained to what extent *variation* may proceed among races which are historically known to have had a common parentage, and what are the circumstances which most favour such variation.—Thirdly, the extreme variations which present themselves among the different races of Men, should be compared with those which occur among tribes of animals known to be of the same parentage; and it should be questioned, at the same time, whether the circumstances which favour the pro-

* "Natural History Review," 1861, p. 489.

duction of varieties in the latter case are in operation in the former.—Fourthly, where it is impossible to trace back distinct races to their origin, it is to be inquired how far agreement in physiological and psychological peculiarities may be regarded as indicating specific identity, even where a considerable difference exists in bodily conformation; and this test, if it can be determined on, has to be applied to Man.—Fifthly, it must be attempted by a detailed examination of the varieties of the Human race themselves, to ascertain whether their differences in conformation are constant: or whether there are not such occasional manifestations in each race, of a tendency to assume the characters of others, as to prevent any definite lines being drawn between the several tribes which together make up the (supposed) distinct species.—An investigation so comprehensive could not be followed out, even in the most cursory manner that would be consistent with utility, within the limits of the present work; and no more will be attempted, therefore, than an indication of the principal points of difference among the several Races of Men, and a statement of the results of inquiry into their degree of constancy in each of the principal groups which they have been thought to mark out.*

787. The differential characters on which those have relied who have sought to establish the existence of a *plurality of species* among Mankind, are both Anatomico-Physiological, and Psychological. Under the former head rank the colour of the Skin, the texture of the Hair, and the conformation of the bony Skeleton, especially the Skull. The latter consist in the superiority claimed for some races over others, in Intellectual power, and in Moral and Religious capacity. The former group will be the one first considered. The *Colour* of the skin exists in the Epidermis only; and it depends upon the admixture of *pigment* cells with the ordinary epidermic cells: all the varied hues presented by the different races of men being due to the relative amount of these cells, and to the particular tint of the pigment which they form. It would be easy, by selecting well-marked specimens of each race, to make it appear that colour affords a character sufficiently distinctive for their separation; thus, for example, the fair and ruddy Saxon, the jet-black Negro, the olive Mongolian, and the copper-coloured North-American, might be considered to be positively separated from each other by this character—propagated, as it seems to be, with little or no perceptible change, from generation to generation. But although such might appear to be the clear and obvious result of a comparison of this kind, yet a more careful and comprehensive survey tends to break down the barrier that would be thus established. For, on tracing this character through the entire family of Man, we find the isolated specimens just noticed to be connected by such a series of links, and the transition from one to the other to be so very gradual, that it is impossible to say where the lines are to be drawn between them. There is nothing here, then, which at all approaches to those fixed and definite marks, that are always held to be requisite for the establishment of specific distinctions among other tribes of animals.

788. But further, there is abundant evidence that these distinctions are far from being constantly maintained, even in any one race. For among all the principal subdivisions, *albinoism*, or the absence of pigment-cells, occasion-

* The whole of this investigation has been most elaborately, and in the Author's opinion most successfully worked out by Dr. Prichard, in his profound and philosophical Treatise on the "Physical History of Man." For a more concise view of Dr. Prichard's argument, with some additional considerations not embraced in it, the Author may refer to his own Article on the 'Varieties of the Human Species,' in the "Cyclop. of Anat. and Phys.," vol. iv.—See also Dr. R. G. Latham's "Natural History of the Varieties of Man;" and his shorter Essay on the 'Varieties of the Human Species,' in Orr's "Circle of the Sciences," vol. i.

ally presents itself; so that the fair skin of the European may present itself in the offspring of the Negro or of the Red man.* On the other hand, instances are by no means rare of the unusual development of pigment-cells in individuals of the fair-skinned races; so that parts of the body are of a dark red or brown hue, or even quite black. Such modifications may seem of little importance to the argument; since they are confined to individuals, and may be put aside as accidental. But there is ample evidence that analogous changes may take place in the course of time, which tend to produce a great variety of shades of colour, in the descendants of any one stock. Thus, in the great Indo-European family (part of the *Caucasian* race of Blumenbach), which may be unquestionably regarded as having had a common origin, we find tribes with fair complexion, yellow hair, and blue eyes—others presenting the xanthous or olive hue—and others decidedly black. A similar diversity may be seen among the American races, which are equally referable to one common stock: and it exists to nearly the same extent among the African nations, which appear to be similarly related to each other. It may be freely admitted that among European colonists settled in hot climates such changes do not present themselves within a few generations; but in many well-known instances of earlier colonization, they are very clearly manifested. Thus the wide dispersion of the Jewish nation, and their remarkable isolation (maintained by their religious observances, from the people among whom they live, render them peculiarly appropriate subjects for such observations; and we accordingly find that the brunette complexion and dark hair, which are usually regarded as characteristic of that race, are frequently superseded, in the Jews of Northern Europe, by red or brown hair and fair complexion; whilst the Jews who settled in India some centuries ago, have become as dark as the Hindoos around them.

789. The relation of the complexions of the different Races of Mankind to the climates they respectively inhabit, which is established by an extended comparative survey of both, leads to the general conclusion that the intertropical region of the earth is the principal seat of the darkest races, whilst the region remote from the tropics is that of the fairer races; and that the climates approaching the tropics are generally inhabited by nations which are of an intermediate complexion. It is important to observe, however, that no regular gradation of tint can be observed in passing from the equatorial to the polar regions. M. Paul Broca† has particularly pointed out that the Esqui-

* A very curious example of *change of colour* in a Negro has been recorded on unquestionable authority.—The subject of it was a negro slave in Kentucky, æt. 45, who was born of black parents, and was himself perfectly black until 12 years of age. At that time a portion of the skin, an inch wide, encircling the cranium just within the edge of the hair, gradually changed to white; also the hair occupying that locality. A white spot next appeared near the inner canthus of the left eye; and from this the white colour gradually extended over the face, trunk, and extremities, until it covered the entire surface. The complete change from black to white occupied about ten years; and but for his hair, which was crisped or woolly, no one would have supposed at this time that his progenitors had offered any of the characteristics of the Negro, his skin presenting the healthy vascular appearance of that of a *fair-complexioned* European. When he was about 22 years of age, however, dark *copper coloured* or brown spots began to appear on the face and hands; but these remained limited to the portions of the surface exposed to light. About the time that the black colour of his skin began to disappear, he completely lost his sense of smell; and since he has become white, he has had measles and hooping-cough a second time. (See Dr. Hutchinson's account of this case in the "Amer. Journ. of Med. Sci.," Jan. 1852.)—A case of partial disappearance of the black colour of the Negro's Skin was brought by Dr. Inman before the Zoological Section of the British Association at Liverpool, Sept. 1854.

† In his Paper 'On Hybridity,' in M. Brown-Séquard's "Journal de la Physiologie" for 1858, p. 462. See for many analogous instances, J. Craufurd, in the "Transactions of the Ethnological Society," vol. i. p. 364.

maux of Greenland, the Lapps and Finns of Europe, and the Samoyedes and Kamschatkans of Asia, all of them nations inhabiting the most northern regions of the habitable globe, present a deep olive complexion, dark straight hair, and dark eyes; being considerably deeper in hue than the Chinese, Burmese, Cochin-Chinese, and Malays, although these are situated so much nearer the equator, and are exposed to the rays of a far fiercer sun. The same conclusion is forced upon us by a survey of the various nations inhabiting the western shores of America; for if we trace them in succession from Behrings Straits to Patagonia, we shall find that under the same latitude as Norway there dwells a race whose colour is yellowish-brown, mixed with red; under that of England a perfectly white race (Vancouver's Islanders), under that of France a red race (Oregon), under that of Spain and Algeria a black race (California.) From thence as far as the equator, under the same latitude as Guinea and Soudan, are races of a merely brown tint, much lighter than the inhabitants of those regions. Lastly, the races which occupy the littoral region extending from the equator to Terra del Fuego, present a brown tint, becoming lighter as the colder regions are approximated; but are suddenly succeeded, under the rigorous climate of Patagonia, by one or more blackish or altogether black races. To these observations it may be added that high mountains, and countries of great elevation, are generally inhabited by people of a lighter colour than are those of which the level is low, such as swampy or sandy plains upon the sea-coast. These distinctions are particularly well seen in Africa, where the tropics almost exactly mark out the limits of the black complexion of the inhabitants; and where the deepest hue is to be seen among the Negroes of the Guinea Coast, whose residence unites both the conditions just mentioned, whilst the mountainous regions in their immediate vicinity are inhabited by tribes of a much lighter aspect.

790. The nature of the *Hair* is, perhaps, one of the most permanent characteristics of different races, and a division has been established between the *Ulotrichi* with crisp or woolly hair, and the *Leiotrichi* with smooth hair. With few exceptions (Andaman Islanders) the *Ulotrichi* are also dolichocephalous. They are represented by the Negroes and Bushmen of Central and Southern Africa, and the Negritos of the Malay Peninsula and Archipelago, and of the Papuan Islands. The *Leiotrichi* are divisible into the Australioid group, the Mongoloid group, the Xanthochroic group (Slavonians, Teutons, Scandinavians), and the Melanochroic group (Iberians and black Celts of Western Europe).* In regard to its colour the same statements apply as those just made with respect to the colour of the skin; the variety of hue being given by pigment-cells, which may be more or less developed under different circumstances. But it has been thought that its *texture* affords a more valid ground of distinction; and it is commonly said that the substance which grows on the head of the African races, and of some other dark-coloured tribes (chiefly inhabiting tropical climates), is *wool* and not hair. This, however, is altogether, a mistake; for microscopic examination clearly demonstrates that the hair of the Negro has exactly the same structure with that of the European, and that it does not bear any resemblance to wool, save in its crispness and tendency to curl. Moreover, even this character is far from being a constant one; for, whilst Europeans are not unfrequently to be met with whose hair is nearly as crisp as that of the Negro, there is a great variety amongst the Negro races themselves which present every gradation, from a completely crisp (or what is termed woolly) hair, to merely curled or even flowing locks.† A

* See Huxley, "The Anatomy of Vertebrated Animals."

† It is a very common mistake, especially in the United States, to consider *Negro*

similar observation holds good in regard to the natives of the islands of the great Southern Ocean, where some individuals possess crisp hair, whilst others of the same race have it merely curled.

791. It has been supposed that varieties in the configuration of the *Skeleton* would afford characters for the separation of the Human races, more fixed and definite than those derived from differences in the form, colour, or texture of the soft parts which clothe it: and attention has been particularly directed to the *skull* and the *pelvis*, as affording such characters. It has been generally laid down as a fundamental principle, that all those nations which are found to resemble each other in the shape of their heads must needs be more nearly related to each other than they are to tribes of Men which differ from them in this particular. But if this principle be rigorously carried out, it will tend to bring together races which inhabit parts of the globe very remote from each other, and which have no other mark of affinity whatever; whilst, on the other hand, it will often tend to separate races which every other character would lead us to bring together. It is to be remembered, moreover, that the varieties in the conformation of the skeleton, presented by the breeds of domesticated animals, are at least equal to those which are manifested in the conformation and colour of their soft parts; and we might reasonably expect, therefore, to meet with similar variations among the Human races. It is probable, however, that climate has not so much influence in producing such changes in the configuration of the body, as the peculiar habits and mode of life of the different races; and Dr. Prichard has pointed out a very remarkable relation of this kind, in regard to the principal types of form presented by the Skull. These differ from each other to such an extent, that if the antero-posterior diameter be taken at 100 the transverse diameter varies from 98 or 99 to 62. The number expressing the proportion of the transverse to the longitudinal diameter of the brain case is termed the cephalic index. Those people who possess crania with a cephalic index of 80 and above are called brachycephali; those with a lower index are dolichocephali.*

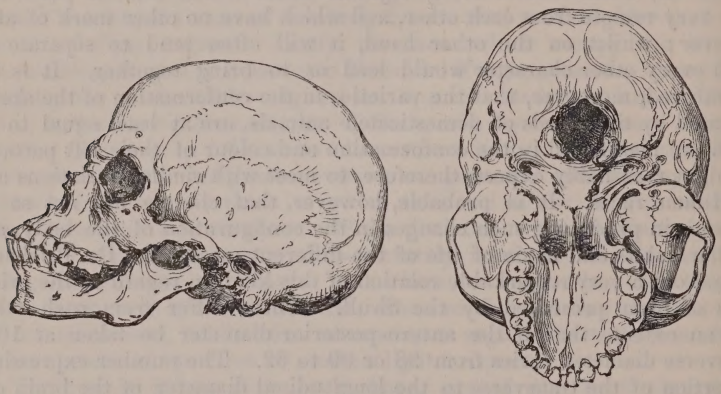
792. Among the rudest tribes of Men, hunters and savage inhabitants of forests, dependent for their supply of food on the accidental produce of the soil, or on the chase—among whom are the most degraded of the African nations, and the Australian savages—a form of head is prevalent which is most aptly distinguished by the term *prognathous*, indicating a prolongation, or forward-extension of the jaws (Fig. 375). This character is most strongly marked in the Negroes of the Gold Coast, whose skulls are usually so formed as to give the idea of lateral compression. The temporal muscles have a great extent, rising high on the parietal bones; the cheek-bones project forward, and not outward; the upper jaw is lengthened and projects forwards, giving a similar projection to the alveolar ridge and to the teeth; and the lower jaw has somewhat of the same oblique projection, so that the upper and lower incisor teeth are set at an obtuse angle to each other, instead of being nearly in parallel planes, as in the European. From the shape of the upper jaw alone would result a marked diminution in the facial angle, measured according to the method of Camper; but this diminution is far from being

as synonymous with *African*. So far is this from being the fact, that, as Dr. Latham justly remarks, "the true Negro area, the area occupied by men of the black skin, thick lips, and woolly hair, is exceedingly small; as small in proportion to the rest of the continent, as the area of the district of the stunted Hyperboreans is in Asia, or that of the Lapps in Europe."

* Huxley, "Anatomy of Vertebrated Animals," p. 495. See also P. Broca, "On Anthropology;" Rolleston and Greenwell, op. cit.; Flower, 'Lectures' in "British Med. Journal," vol. i. 1879.

sufficient to approximate the Ethiopian races to the higher Apes, as some have supposed it to be. Independently of the diminution of the facial angle resulting from the projection of the upper jaw, it is quite certain that in the typical prognathous skull there is a want of elevation of the forehead; but it does not appear that there is a corresponding diminution in the capacity of the cranial cavity, the retreating form of the forehead being partly due to the general elongation of the skull in the antero-posterior direction. Nor is it true, as stated by some, that the position of the foramen magnum in the Negro is decidedly behind that which it holds in the European, in this respect approaching that of the Apes; since, if due allowance be made for the projection of the upper jaw, this aperture is found to have the same position

Fig. 375.



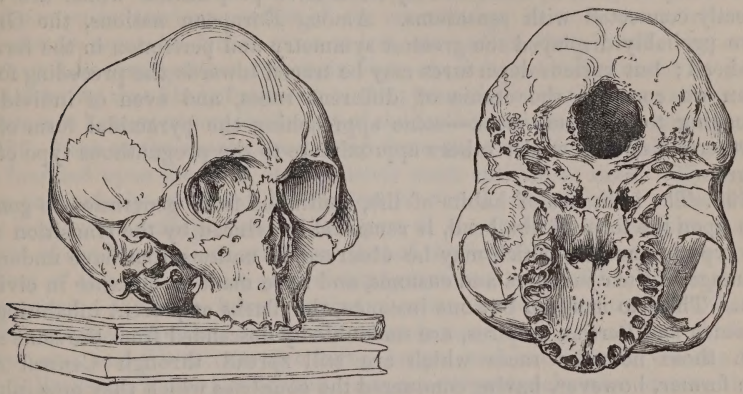
Profile and basal views of the *Prognathous Skull* of a Negro.

in the prognathous skull as in the oval one—namely, exactly behind the transverse line bisecting the antero-posterior diameter of the base of the cranium. The prognathous skull is further remarkable for the large development of the parts connected with the organs of sense, especially those of smell and hearing. The aperture of the nostrils is very wide, and the internal space allowed for the distribution of the olfactory nerve is much larger than in most European heads; the posterior openings of the nasal cavity are not less remarkable for their width than the anterior. The external auditory meatus is also peculiarly wide and spacious; and the orbital cavities have been thought to be of more than ordinary capacity—but this last is by no means a constant character.

793. A second type of cranial conformation, very different from the preceding, belongs principally to the nomadic races which wander with their herds and flocks over vast plains; and to the tribes which creep along the shores of the Icy Sea, and live partly by fishing, and in part on the flesh of their reindeer. This form, designated by Dr. Prichard as the *pyramidal* (Fig. 376), is typically exhibited by various nations of Northern and Central Asia; and is seen in an exaggerated degree in the Esquimaux. Its most striking character is the lateral or outward projection of the zygoma, which is due to the form of the malar bones. These do not project forwards and downwards under the eyes, as in the prognathous skull; but take a lateral or outward direction, forming, with the zygomatic process of the temporal bone, a large rounded sweep or segment of a circle. From this, in connection with the narrowness of the forehead, it results that lines drawn from the zygomatic

arches, touching the temples on either side, instead of being parallel (as in Europeans), meet over the forehead, so as to form with the basis a triangular figure. The upper part of the face being remarkably flat, the nose also being flat, and the nasal bones, as well as the space between the eyebrows, being nearly on the same plane with the cheek-bones, the triangular space bounded

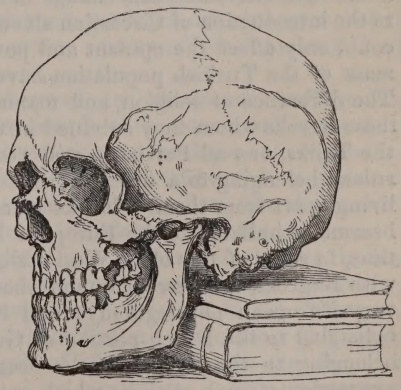
Fig. 376.



Front and basal views of the *Pyramidal Skull* of an Esquimaux.

by these lines may be compared to one of the faces of a pyramid. The orbits are large and deep; and the peculiar conformation of the bones which surround it, gives to the aperture of the lids an appearance of obliquity—the inner angle seeming to be directed downwards. The whole face, instead of presenting an oval form, as in most Europeans and Africans, is of a lozenge-shape. The greater relative development of the zygomatic bones, and of the bones of the face altogether, when compared with the capacity of the cranium, indicates in the pyramidal skull a more ample extension of the organs subservient to sensation; the same effect being thus produced by lateral expansion, as by the forward extension of the facial bones in the prognathous skulls.

Fig. 377.



Oval Skull of a European.

794. The most civilized races—those which live by agriculture and the arts of cultivated life—all the most intellectually-improved nations of Europe and Asia—have a shape of the head which differs from both the preceding, aud which may be termed the *oval* or *elliptical*. This at once approves itself as a more symmetrical form, no part having an excessive prominence; whilst, on the other hand, there is nowhere an appearance of undue flattening or compression. The head is altogether of a rounder shape than in the other varieties, and the forehead is more expanded; while the maxillary bones and the zygomatic arches are so formed as to give the face an oval shape, nearly on a plane with the forehead and cheek-bones, and not projecting towards the

lower part. Owing to the more perpendicular direction of the alveolar processes, the front teeth are fixed in planes which are nearly or quite parallel to each other. The principal features in this form of cranium are thus of a negative character; the chief positive distinction is the large development of the cranial cavity, and especially the fulness and elevation of the forehead, in proportion to the size of the face; indicating the predominance of the intellectual powers over those merely instinctive propensities which are more directly connected with sensations. Among European nations, the Greeks have probably displayed the greatest symmetry and perfection in the form of the head; but various departures may be traced towards the preceding forms, when we compare the crania of different races, and even of individuals, belonging to the same stock—some approaching the pyramidal form of the Northern Asiatics, whilst others approximate to the prognathous type of the Negro.

795. The influence of habits of life, continued from generation to generation upon the form of the head, is remarkably evinced by the transition from one type to another, which may be observed in nations that have undergone a change in their manners and customs, and have made an advance in civilization. Thus, to mention but one instance, the Turks at present inhabiting the Ottoman and Persian empires, are undoubtedly descended from the same stock with those nomadic races which are still spread through Central Asia. The former, however, having conquered the countries which they now inhabit, eight centuries since, have gradually settled-down to the fixed and regular habits of the Indo-European race, and have made corresponding advances in civilization; whilst the latter have continued their wandering mode of life, and can scarcely be said to have made any decided advance during the same interval. Now the long-since-civilized Turks have undergone a complete transformation into the likeness of Europeans; whilst their nomadic relatives retain the pyramidal configuration of the skull in a very marked degree. Some have attributed this change in the physical structure of the Turkish race to the introduction of Circassian slaves into the harems of the Turks; but this could only affect the opulent and powerful amongst the race; and the great mass of the Turkish population have always intermarried among themselves. The difference of religion and manners must have kept them separate from those Greeks whom they subdued in the new Ottoman countries; as in Persia, the Tajiks, or real Persians, still remain quite distinct from their Turkish rulers, belonging to a different sect among the Mussulmans, and commonly living apart from them.—In like manner, even the Negro head and face may become assimilated to the European by long subjection to similar influences; thus, in some of our older West Indian Colonies, it is not uncommon to meet with Negroes, the descendants of those first introduced there, who exhibit a very European physiognomy; and it has even been asserted that a Negro belonging to the Dutch portion of Guiana may be distinguished from another belonging to the British settlements, by the similarity of the features and expression of each to those which respectively characterize his masters. The effect could not be here produced by the intermixture of bloods, since this would be made apparent by alteration of colour.—But not only may the pyramidal and prognathous types be elevated towards the elliptical; the elliptical may be degraded towards either of these. Want, squalor, and ignorance have a special tendency to induce that diminution of the cranial portion of the skull, and that increase of the facial, which characterize the prognathous type; as cannot but be observed by any one who takes an accurate and candid survey of the condition of the most degraded part of the

population of the great towns of this country, but as is seen to be pre-eminently the case with regard to the lowest classes of Irish immigrants.* A certain degree of retrogression to the pyramidal type is also to be noticed among the nomadic tribes which are to be found in every civilized community. Among these, as has been remarked by a very acute observer,† "According as they partake more or less of the purely vagabond nature, doing nothing whatsoever for their living, but moving from place to place, preying on the earnings of the more industrious portion of the community, so will the attributes of the nomad races be found more or less marked in them; and they are all more or less distinguished for their high cheek-bones and protruding jaws;" thus showing that kind of mixture of the pyramidal with the prognathous type, which is to be seen among the lowest of the Indian and Malayo-Polynesian race.

796. Next to the characters derived from the form of the head, those which are founded upon the form of the *pelvis* seem entitled to rank. These have been particularly examined by Professors Vrolik and Weber. The former was led, by his examinations of this part of the skeleton, to consider that the pelvis of the Negress, and still more that of the female Hottentot, approximates to that of the Simiæ in its general configuration; especially in its length and narrowness—the iliac bones having a more vertical position, so that the anterior spines approach one another much more closely than they do in the European; and the sacrum also being longer and narrower. On the other hand, Professor Weber‡ concludes, from a more comprehensive survey, that no particular figure is a permanent characteristic of any one race. He groups the principal varieties which he has met with, according to the form of the upper opening into oval, round, four-sided, and wedge-shaped. The first of these is most frequent in the European races; the second, among the American races; the third, most common among the Mongolian nations, corresponds remarkably with their form of head; whilst the last chiefly occurs among the races of Africa, and is in like manner conformable with the oblong compressed form usually presented by their cranium. But although there are particular shapes which are most prevalent in each race, yet there are numerous individual deviations of such a nature that every variety of form presents itself occasionally in any given race.

797. Other variations have been observed by anatomists, between the different races of Mankind, in the relative length of the bones, and in the shape of thel imbs; but these also seem to have reference to the degree of civilization, and to the regularity of the supply of wholesome nutriment. It is generally to be observed that the races least improved by civilization, like the uncultivated breeds of animals, have slender, lean, and elongated limbs; this may be especially remarked in the natives of Australia. In nearly all the less civilized races of Men, the limbs are more crooked and badly-formed than the average of those of Europeans; and this is particularly the case in the Negro, the bones of whose legs bow outwards, and whose feet are remarkably flat. It has been generally believed that the length of the fore-arm in the Negro is much greater than in the European, as to constitute a real character of approximation to the Apes. The difference, however, is in reality extremely slight; and is not at all comparable with that which exists between the most uncultivated races of Men and the highest Apes. And in regard to all the peculiarities here alluded to, it is to be observed that they can only be

* See the "Dublin University Magazine," No. xlviii.

† Mr. Henry Mayhew, in "London Labour and the London Poor," p. 2.

‡ "Die Lehre von den Ur- und Racenformen der Schaedel und Becken des Menschen," Düsseldorf, 1830.

discovered by the comparison of large numbers of one race with corresponding numbers of another; for individuals are found in every tribe, possessing the characters which distinguish the majority of the other race. Such peculiarities, therefore, are totally useless as the foundation of *specific* characters; being simply variations from the ordinary type, resulting from causes which might affect the entire race as well as individuals.—The connection between the general form of the body, on the one hand, and the degree of civilization (involving the regular supply of nutriment) on the other, is made apparent, not merely by the improvement which we perceive in the form, development, and vigour of the frame, as we advance from the lowest to the most cultivated of the Human race; but also by the degradation that is occasionally to be met with in particular groups of the higher tribes, which have been subjected for several generations to the influence of depressing causes. Of such degradation, occurring under circumstances that permit its successive steps to be traced, we have a remarkable example in the conversion of certain tribes of the Hottentot race into Bushmen; and there is very strong ground for the belief that similar influences have operated at a more remote period, in the production of the peculiar characters of the Guinea-coast Negroes and Australian Bushmen.

798. Independently, however, of the obvious modifying influence of external circumstances, much allowance must be made for that *tendency to variation*, which presents itself, more or less, in all those races of animals which possess such a constitutional capability of adaptation to changes in climate, habits of life, &c., as enables them to live and flourish under a variety of conditions. Thus we find that the offspring of any one pair of domesticated animals do not all precisely agree among themselves, or with their parents, either in bodily conformation or in psychical character; but that *individual* differences, as they are termed, exist among them. Now, as this tendency to variation cannot be clearly traced to any influence of external circumstances, it is commonly distinguished by the term 'spontaneous;' but as there is no effect without a cause, and as the widest differences of this kind present themselves in those races which are most obviously amenable to the influence of external conditions, we seem justified in attributing them to agencies operating unostensibly upon the parents, either previously to their intercourse, or at the time of coition (§ 725), or in the female during the period of utero-gestation (§ 728). The difference between wild and domesticated animals in regard to *colour* affords a very good illustration of this general fact; for the uniformity among the former is no less remarkable than the want of constancy among the latter; and whilst variety of colour soon gives place to uniformity, when domesticated races return in any inconsiderable degree towards their primitive state,* it very speedily develops itself in races which are undergoing the converse process.†

799. Now it is by taking advantage of those 'spontaneous' departures from the ordinary type, which present features of value to the breeders of domesticated animals, that *new races* are developed from time to time among these; any strongly marked peculiarity which thus appears in only a single individual, being usually transmitted to some of its offspring, and being almost certainly

* This has been especially noticed in the dogs, horses, cattle, sheep, and hogs introdueed by the Spaniards into South America.

† Thus, Mr. T. Bell informs us ("British Quadrupeds," 2nd edit., p. 203), that an Australian bitch, or dingo, in the Zoological Gardens, had a litter of puppies, the father of which was also of that breed; both parents had been taken in the wild state, both were of the uniform reddish-brown colour which belongs to the race, and the mother had never bred before; but the young, generated in confinement, and in a half-domesticated state, were all more or less spotted.

perpetuated when *both* parents are distinguished by it, as happens when the products of the first procreation become capable of breeding with each other.*—Now there can be no hesitation in admitting, that the tendency to the so-called 'spontaneous' variation prevails in the Human race to a greater degree than in any other; since we find most remarkable diversities in features, complexion, hair, and general conformation, among the offspring of the same parentage; whilst more special modifications of the ordinary type, such as the possession of six fingers on each hand and of six toes on each foot are of no unfrequent occurrence. Under ordinary circumstances, these modifications tend to disappear as often as they occur; the free intermixture of those members of the race which possess them, with those which depart less from the ordinary type, tending to merge them in the general average. But there can be no reasonable doubt that if the same kind of segregation were practised among Mankind, which is adopted by the breeders of animals for the purpose of perpetuating a particular variety—if, for example, the members of a six-fingered family were to intermarry exclusively with one another—any such variety would be permanently established as a new race. Now if it be borne in mind that the influence of a scanty population, in the early ages of the Human race, by isolating different families from each other, and causing inter-marriages among even the nearest relatives, would have been precisely the same with that which is now exercised by the breeders of animals, we see one reason why the varieties which *then* arose should have a much greater tendency to self-perpetuation than those which *now* occasionally present themselves. And when, too, it is borne in mind, that the change in external conditions induced by migration would thus operate not only upon the parents but upon the offspring, and would have a continual influence in so modifying the constitution of the latter that the peculiarities thus acquired by them would be transmitted in yet greater intensity to their progeny, there is no real difficulty in accounting, upon the strictest physiological principles, for the widest of those departures from one common type of conformation, which we encounter in our survey of the different Races of Mankind.†

800. Hence we are led to conclude, that, so far as regards their Anatomical structure, there is no such difference among them as would justify to the Zoologist the assertion of their distinct origin. But further, although the comparison of the structural characters of the Human races does not furnish any positive evidence of their descent from a common stock, it justifies the assertion that even if their stocks *were* originally distinct, there could have been no essential difference between them; the descendants of any one such stock being able to assume the characters of another. This, as already remarked, can be proved by historical evidence in regard to a sufficient number

* See the history of the introduction of the *ancon* breed of sheep, characterized by a peculiar conformation of its limbs, in Massachussetts, given by Col. Hutchinson in the "Phil. Trans." for 1813.—A similar account was subsequently given by Prof. Owen (in a Lecture delivered before the Society of Arts, Dec. 10, 1851), respecting the recent introduction of a new breed of merino sheep, distinguished for the long, smooth, straight, and silky character of the wool, and now known as the *Mauchamp* breed.—In both instances, the breed originated in the spontaneous appearance of a male lamb possessing the peculiarities in question; from its offspring such a selection was made by the breeder, as enabled him to bring together males and females, both of which were distinguished by them; and in their progeny, the peculiarities uniformly appeared.

† For a masterly digest of the analogical evidence furnished by the changes known to have been thus produced among domesticated animals, and of the modifications which particular tribes of men can be shown to have undergone within the historic period, see Dr. Prichard's "Physical History of Mankind," and his "Natural History of Man;" see also the summary given by the Author in the "Cyclop. of Anat. and Physiol.," vol. iv. pp. 1301—1339; and Darwin, "The Variation of Animals and Plants under Domestication," 1868.

of tribes, to justify the same assertion with respect to others, whose languages, customs, habits of thought, &c., have an affinity strong enough to warrant us in regarding them as descendants of the same stock, whilst their physical conformation is widely different. Each principal geographical area, which is so isolated from others as to render it probable, *à priori*, that its population has extended from one centre—such as the Continent of Africa, or America—contains races of very diversified physical characters, whose linguistic affinities make it almost certain that they must have had a common descent; and thus, in whatever mode the types of the principal varieties are selected, they are found to be connected by so gradual a series of intermediate or transitional forms, that it is impossible to draw any such line of demarcation between them, as would be required by a soundly-judging Naturalist for the boundary of distinct species.

801. A very important confirmation of this view is afforded by the essential agreement which exists among the different Races of Mankind in regard to their Physiological history; the variations which they present not being greater than those which we meet with between the different individuals of any one race. Thus, we not only find the average duration of life to be the same (making allowance for circumstances which are likely to induce disease), but the various epochs of life such as the times of the first and second dentition, the period of puberty, the duration of pregnancy, the intervals of the catamenia, and the time of their final cessation—present a marked general uniformity, such as does not exist among similar epochs in the lives of species that are nearly allied but yet unquestionably distinct. Further, the different races of Mankind are all subject to the same diseases, both sporadic, endemic, and epidemic; the only exceptions being those in which the constitution of the race has *grown to* a certain set of influences (as that of the Negro to the malaria which generate certain pernicious fevers in the European), producing an hereditary immunity in the race, which is capable of being acquired by individuals of other races, by a process of acclimatization commenced sufficiently early.*—The most important physiological test, however, of specific unity or diversity, is that furnished by the Generative process. It may be considered as a fundamental fact, alike in the Vegetable and in the Animal kingdom, that *hybrid* races originating in the sexual connection of individuals of two different *species*, do not tend to self-perpetuation; the hybrids being nearly sterile with each other, although they may propagate with either of their parent-races, in which the hybrid race will soon merge; whilst, on the other hand, if the parents be themselves *varieties* of the same species, the hybrid constitutes but another variety, and its powers of reproduction are rather increased than diminished, so that it may continue to propagate its own race, or may be used for the production of other varieties, almost *ad infinitum*. It appears that, among

* This view of the immunity of the Negro race from certain forms of fever which are very fatal to Europeans, is justified, the Author believes, by all the facts known upon the subject. Much may be set down, as he is assured by Dr. Daniell, to the better adaptation of the Negro habits of life to their climate; and Europeans who exercise due caution (especially in regard to the functions of the skin), may preserve an immunity scarcely less complete. Dr. Daniell himself, having been taken prisoner by one of the Negro tribes at an early age, and having spent two years among them, seems to have been thoroughly acclimatized; and has subsequently passed many years on the most unhealthy parts of the coast, without experiencing any severe attacks of illness, and in the enjoyment of very good general health.—It is sometimes maintained that the Negro race possesses such a complete exemption from the Yellow Fever of the United States as marks its specific difference; such, however, is not constantly the case, since Negroes occasionally suffer from it; and their *comparative* immunity seems fairly attributable to the constitutional peculiarity *acquired* by their African progenitors, and capable of being acquired by Europeans also.

Plants, hybrids originating between undoubtedly distinct species, sometimes reproduce themselves for two or three generations, but do not continue beyond the fourth. Amongst animals, the limits of hybridity between parents of distinct species are more narrow, since the hybrid is totally unable to continue its race with one of its own kind;* and although it may propagate with one of its parent-species, the progeny will of course approach in character to the pure breed, and the race will speedily merge into it. In Animals, as among Plants, the mixed offsprings originating from different races within the limits of the same species generally *exceed* in vigour, and in the tendency to multiply, the parent-races from which they are produced, so as to gain ground upon the older varieties, and gradually to supersede them. In this manner, by the *crossing* of the breeds of our domesticated animals, many new and superior varieties have been produced. The general principle is, then, that beings of distinct *species*, or descendants from stocks originally different, cannot produce a mixed race which shall possess the capability of perpetuating itself; whilst the union of *varieties* has a tendency to produce a race superior in energy and fertility to its parents.—The application of this principle to the Human races leaves no doubt with respect to their specific unity; for, as is well known, not only do all the races of men breed freely with each other, but the mixed race is generally superior in physical development, and in tendency to rapid multiplication, to either of the parent stocks; so that there is much reason to believe that, in many countries, the mixed race between the Aborigines and European colonizers will ultimately become the dominant power in the community. This is especially the case in India, South America, and Polynesia.

802. The question of *Psychical* conformity or difference among the Races of Mankind, is one which has a most direct bearing upon the question of their specific unity or diversity; but it has an importance of its own, even greater than that which it derives from this source. For, as has been argued with great justice and power,† the real Unity of Mankind does not lie in the consanguinity of a common descent, but has its basis in the participation of every race in the same moral nature, and in the community of moral rights, which hence becomes the privilege of all. "This is a bond which every man feels more and more the farther he advances in his intellectual and moral culture, and which in this development is continually placed upon higher and higher ground: so much so that the physical relation arising from a common descent is finally lost sight of, in the consciousness of the higher moral obligations." It is in these obligations, that the moral *rights of men* have their foundation; and thus, "while Africans have the hearts and consciences of human beings, it could never be right to treat them as domestic cattle or as wild fowl, if it were ever so abundantly demonstrated that their race was but an improved species of ape, and ours a degenerate kind of god."—The Psychical comparison of the various Races of Mankind is really, therefore, in a practical point of view, the most important part of the whole investigation; but it has been, nevertheless, the one most imperfectly pursued, until the inquiry was taken up by Dr. Prichard. The mass of evidence which he has accumulated on this subject, however, leaves no reasonable doubt that no more "impassable barrier" really exists between the different races with respect to this, than in

* One or two instances have been stated to occur in which a Mule has produced offspring from union with a similar animal; but this is certainly the extreme limit, since no one has ever maintained that the race can be continued farther than the second generation without admixture with one of the parent species. See also Darwin "On the Variations of Plants and Animals under Domestication."

† See the "New Quarterly Review," No. xv. p. 131; and an Article by Prof. Agassiz in the "Christian Examiner," Boston (N.E.), 1850.

regard to any of those points of ostensible diversity which have been already considered; the variations in the positive and relative development of their respective psychical powers and tendencies, not being greater, either in kind or degree, than those which present themselves between individuals of our own or of any other race, by some members of which a high intellectual and moral standard has been attained. The tests by which we recognize the claims of the outcast and degraded of our own or of any other 'highly-civilized' community, to a common humanity, are the same as those by which we should estimate the true relation of the Negro, the Bushman, or the Australian, to the cultivated European. If, on the one hand, we admit the influence of want, ignorance, and neglect, in accounting for the debasement of the savages of our own great cities—and, if we witness the same effects occurring under the same conditions among the Bushmen of Southern Africa (§ 812)—we can scarcely hesitate in admitting, that the long-continued operation of the same agencies has had much to do with the psychical as well as the physical deterioration of the Negro, Australian, and other degraded races. So, on the other hand, if we cherish the hope that the former, so far from being irreclaimable, may at least be brought-up to the standard from which they have degenerated, by means adapted to develop their intellectual faculties and to call forth the higher parts of their moral nature, no adequate reason can be assigned why the same method should not succeed with the latter, if employed with sufficient perseverance. It will be only when the effect of education, intellectual, moral, and religious, shall have been fairly tested by the experience of *many generations*, in conjunction with the influence of a perfect equality in civilization and social position, that we shall be entitled to speak of any essential and constant psychical difference between ourselves and the most degraded beings clothed in human form. All the evidence which we at present possess leads to the belief, that under a vast diversity in degree and in modes of manifestation, the same intellectual, moral, and religious *capabilities* exist in the Races of Mankind; so that, whilst we may derive from this conformity a powerful argument for their Zoological Unity as a species, we are also directly led to recognize their community of moral nature with ourselves, and to admit them to a participation in our own rights.

803. Most important assistance is afforded in the determination of the real affinities of different Races, by the study of their *Languages*. This, however, is a department of the inquiry so far beyond the limits of Physiological science that it must be here dismissed with a bare mention of those results, to which the zealous pursuit of it by a large number of philosophic Philologists seems undoubtedly to tend.—There can be no reasonable doubt that, as a general principle, the affinities of races are more surely indicated by their languages than by their physical features; and the experienced philologist is generally able to discriminate those resemblances, which may have arisen out of the introduction of words or of modes of construction from the one into the other, by conquest, commercial intercourse, or absolute intermixture, from those which are the result of a community of origin. And thus are supplied those means of tracing the past history of races, which are seldom afforded by written records, or even (at least with any degree of certainty) by traditional information.* It is to be borne in mind that the affinities of languages are indicated, not merely by verbal resemblance, but by the similarity of their modes of grammatical construction, or the methods by which the relation between different words that constitute sentences is indicated. The most positive evidence is of course afforded, when a conformity exists both in the

* See, however, Dr. E. B. Tylor's "Primitive Culture."

vocabularies and in the *modes of construction* of two languages; but it frequently happens that although the conformity exists in regard to one of these alone, yet the evidence which it affords is perfectly satisfactory. Thus, there are many cases in which the vocabularies are so continually undergoing important changes (the want of written records not permitting them to acquire more than a traditional permanence), that their divergence becomes so great, even in the course of a few generations, as to prevent tribes which are by no means remotely descended from a common ancestry, from understanding one another; whilst yet the system of grammatical construction, which depends more upon the grade of mental development and upon habits of thought, exhibits a remarkable permanence. Such appears to be true of the entire group of American languages; which seem, as a whole, to be legitimately referable to a common stock, notwithstanding their complete verbal diversity. On the other hand, when two languages or groups of languages differ greatly in construction, but present that kind of verbal correspondence on which the philologist feels justified in placing most reliance (namely, an essential conformity in those 'primary words' which serve to represent the universal ideas of a people in the most simple state of existence), that correspondence may be held to indicate a community of origin, if it can be proved that it has not been the result of intercourse between the two families of nations subsequently to their first divergence, and if it seems probable on other grounds that their separation took place at a period when as yet the grammatical development of both languages was in its infancy. Such appears to have been the case with certain of those groups of languages whose distinctness can be traced back historically for the longest period.*—It is evident, then, that Philological inquiry must be looked to as one of the chief means of determining the question of radiation from a *single* centre or from *multiple* centres; and it is a remarkable fact, that the linguistic affinity and the conformity in physical characters frequently stand in a sort of complemental relation to each other, each being the strongest where the other is weakest; so that, by one or other of these links of connection, a close relationship is indicated between all those families of nations under which the several races appear to be most naturally grouped.

2. *General Survey of the Principal Varieties of the Human Species.*

804. The distribution of the Races of Mankind under five primary varieties, according to their respective types of cranial conformation, as first proposed by Blumenbach, is still so commonly received, notwithstanding the distinct proof which has been given of the fallacious nature of its basis, that it will be desirable to explain his terms, and at the same time to show how far the information subsequently acquired has tended to modify his arrangement.—The first of these varieties, which is considered to be distinguished by the possession of the *oval* or *elliptical*† type of cranial conformation, was designated *Caucasian* by Blumenbach, on two grounds; first, because he considered the

* The changes, or stages of growth and development, through which all languages probably pass have been traced in a most interesting manner by Prof. Max Müller, in his "Lectures on the Science of Language" 1861: see Lectures ii. and viii.

† Now generally termed dolichocephalic, from δολιχός, long, and κεφαλή, head; in opposition to brachycephalic, from βραχύς, short, and κεφαλή (§ 790). According to Retzius, the majority of the people of *Western Europe* are dolichocephalic and orthognathic (ὀρθός, upright, and γνάθος, jaw); whilst the brachycephalic is the prevalent form of the skull throughout the great extent of *Eastern Europe*. He regards the Hindoos, Arian Persians, Arabs, and Jews, with the Tungusians and Chinese, as being examples of *Asiatic* dolichocephali, the last two being prognathic (πρό, forwards, and γνάθος, jaw), the former orthognathic; whilst the Samoyedes, Turks, Circassians, Afghans, Lascars, Tartars, Mongolians (both of Asiatic Russia and

Caucasian people (of whom the Georgians and Circassians are the best known examples) as presenting its physical characters in the greatest perfection; and second, because it was supposed that the Caucasian range of mountains might be regarded as the centre or focus of the races belonging to it. Neither of these ideas, however, is correct; for whilst the oval form of cranium is presented with fully as great beauty and symmetry by the Greeks, it seems now to be almost certainly determinable by the evidence of language, that the Georgian and Circassian nations are really of Mongolian origin, and consequently have no direct relation or affinity with the other nations usually ranked as belonging to this variety; and the evidence of history and tradition, so far from pointing to the Caucasian range as the original centre of radiation of the race, accords with that of language in assigning its locality much nearer to Central Asia. It would be most desirable, therefore, that some other designation should be substituted for that given by Blumenbach; were it not that the present state of our knowledge requires the entire abandonment of his doctrine, that the races agreeing in this type of conformation are mutually connected by community of descent. For, even within the limits of Europe, we find at least two nations—the Turks, and the Magyars or true Hungarians (§ 807)—whose crania are characteristically oval, and which are yet undoubtedly of Mongolian origin; and although some allowance must be made, in regard to the change which has taken place among the former, for the influence of intermixture, with other races, yet there is no reason to believe that any such influence has operated among the Magyars, whose blood seems to have been transmitted with remarkable purity from the time when they settled in Hungary about ten centuries since. In Asia, we find this type presented not merely by the Persian and other Indo-European races, but also by the Syro-Arabian and by the larger proportion of the inhabitants of Hindostan; yet the Syro-Arabian races are more nearly related to the African stock (§ 806) than to that from which most of the present inhabitants of Europe have sprung; and there is good reason to believe that the great mass of the existing inhabitants of India are of Mongolian descent (§ 807). It will be necessary, therefore, to consider the nations which present the so-called Caucasian type of cranial conformation under several distinct heads. No uniformity exists amongst them in regard to *colour;* for this character presents every intermediate gradation between the fair and florid tint, with light red or auburn hair, of the Northern European, to the dusky or even black hue of the races bordering on or lying between the Tropics. The hair is generally long and flexible, with a tendency to curl; but considerable variety presents itself with regard to this particular. The conformation of the features approaches more or less closely to that which we are accustomed to regard as the type of beauty.

805. The first place, in a more natural distribution of the Human Races, must undoubtedly be given to that which is designated by Dr. Prichard as the *Aryan*, and which is often termed the *Indo-European;* including the collective body of European nations, with the Persians,* Afghans, and certain

Mongolia), and Malays, are all prognathic brachycephali, and constitute the prevailing type. On the continent of Australia and in Van Diemen's Land, all the savage tribes are prognathic dolichocephali. See his 'Glance at the present state of Ethnology with reference to the Form of the Skull,' in the "Medico-Chir. Rev." for 1860, vol. xxv. p. 503, and vol. xxvi. p. 215.

* The modern Persians are a very mixed race, in which Turkish and Arab elements largely participate. The most perfect representatives of the original stock (whose purity of descent seems to have been maintained from the time of their original migration into their present locality, by the physical obstacles which have cut them off from intercourse with their nearest neighbours) are believed to be the Kafirs of Kafirstan, a fair-skinned, light-

other nations of the south-western portion of the Asiatic continent,* near to which their original focus appears to have been. The great bond of connection between these nations, lies in their languages; which, in spite of great diversities, present a certain community of character that is recognised by every philologist. The family which is most dissimilar to the rest (the typical Celt contrasting remarkably with the types of the Germanic group, both in physical conformation and in psychical characters) is that formed by the *Celtic* nations: but these are undoubtedly, like the others, of Eastern origin, as was first shown by Dr. Prichard;† though they appear to have detached themselves from the common stock at an earlier period in the development of its language. The *Indo*-Germanic languages are obviously all formed upon the same base with the ancient Sanskrit, if not upon the Sanskrit itself; and they are united alike by community in many of the most important 'primary words,' and by general similarity in grammatical construction. The existing Lettish or Lithuanian dialect presents a very near approach to the original type; and the Old Prussian, a dialect spoken as late as the sixteenth century, had a still closer alliance to the ancient Zend or Median, which seems to have been a very early derivation from the Sanskrit, and which is the basis of the language now spoken in Persia.—But there is evidence that, notwithstanding the mutual affinities of the Indo-Germanic languages, every one of them has been modified by the introduction of extraneous elements; thus, in those of Western Europe, there is a considerable admixture of Celtic; whilst in others there are traces of more barbaric tongues. In fact, there can be little doubt that Europe had an indigenous population, before the immigration of the Indo-German or even of the Celtic tribes; and of this population it seems most probable that the Lapps and Finns of Scandinavia, and the Euskarians (or Basques) of the Biscayan provinces, are but the remnant. The former of these tribes, which is undoubtedly of Mongolian origin, once extended much farther south than at present; and with regard to the latter, whose nearest linguistic affinities are also with the tongues of High Asia, there is ample historical proof that they had formerly a very extensive distribution through Southern Europe. It would not seem improbable, then, that the advance of the Indo-European tribes from the south-east corner into Central Europe, separated that portion of the aboriginal (Mongolian) population which they did not absorb or destroy, into two great divisions; of which one was gradually pressed northward and eastward, so as to be restricted to Finland and Lapland; and the other southward and westward, so as to be confined at the earliest historic period to a part of the peninsula of Spain and the South of France, gradually to be driven before the successive irruptions of the Celts, Romans, Arabians, and other nations, until their scanty remnant found an enduring refuge in the fastnesses of the Pyrenees.‡—The Indo-Germanic race is unquestionably that which has exercised the greatest influence on the civilization of the Old World; and it seems indubitably destined to acquire a similar influence in

haired race inhabiting the impracticable mountain country on the watershed between the Oxus and the north-western sources of the Indus. The Tajiks of Bokhara also keep up the ancient lineage and language, although their country is ruled by people of Turkish descent.

* The population of Hindostan has been commonly accounted as belonging to this division; but the more intimate the knowledge attained of its character and langages, the more does it lead to the conclusion that the great mass of this population is really of Mongolian descent (§ 808).

† "On the Eastern Origin of the Celtic Nations," 1831.

‡ This view, which was suggested by the Author in the "Brit. and For. Med. Rev.," Oct. 1847, without the knowledge that it had been elsewhere propounded, has been put forth with considerable confidence by Dr. Latham ("Varieties of Man," 1850), as having originated with Arndt and been adopted by Rask, distinguished Scandinavian ethnologists.

those newly-found lands which have been discovered by its enterprise. With scarcely an exception, as Dr. Latham has justly remarked, the nations belonging to it present an *encroaching* frontier; there being no instance of its permanent displacement by any other race, save in the case of the Arab dominion in Spain, which has long since ceased; in that of the Turkish dominion in Turkey and Asia Minor, which is evidently destined to expire at no distant period, being upheld for merely political purposes by extraneous influence; and in that of the Magyars in Hungary, who only maintain their ground through their complete assimilation to the Indo-Germanic character. It is a remarkable fact, that in most cases in which this race extends itself into countries previously tenanted by people of an entirely different type, the latter progressively decline and at last disappear before it, provided the climate be such as enables it to maintain a vigorous existence; this is pre-eminently the case in North and South America, in Australia, in New Zealand, and in many of the smaller Polynesian islands. And where the climate is less favourable to the perpetuation of the race in its purity, an intermixture with the native blood frequently gives origin to a mixed race, which possesses the developed intellect of the one, and the climatic adaptiveness of the other, and which appears likely ultimately to take the place of both.

806. The *Syro-Arabian* or *Semitic* nations agree with the preceding in general physical characters, but differ entirely in the structure of their language, and for the most part in vocabulary also, though recent researches seem to indicate that certain *roots* of the Semitic and Indo-Germanic languages have a decided affinity. It seems quite certain, however, that the linguistic affinities of the Semitic nations are rather with the *African* than with the Indo-European races; and so strong is the link of connection thus established, that by Dr. Latham they are ranked with the former under the general designation *Atlantidæ*,* whilst Mr. Norris, whose authority upon all such subjects is deservedly great, is strongly disposed (as he has himself informed the Author) to consider them an *essentially African* people.—The original seat of this race, however, is commonly reputed to have been that region of Asia which is intermediate between the countries of the Indo-European and of the Egyptian races; having as its centre the region watered by the great rivers of Mesopotamia. Several of the nations primarily constituting this group have become extinct, or nearly so; and the *Arabs*, which originally formed but one subdivision of it, have now become the dominant race, not only throughout the ancient domain of the the Syro-Arabian nations, but also in Northern Africa. In the opinion of Baron Larrey, who had ample opportunities for observation, the skulls of the Arabian race furnish, at present the most complete type of the human head; and he considered the remainder of the physical frame as equally distinguished by its superiority to that of other races of men. The different tribes of Arabs present very great diversities of colour, which are generally found to coincide with variations in climate. Thus, the Shegya Arabs, and others living on the low countries bordering on the Nile, are of a dark brown or even black hue; but even when quite jetty, they are distinguished from the Negro races by the brightness of their complexions, by the length and straightness of their hair, and by the regularity of their features. The same may be said of the wandering Arabs of Northern Africa; but the influence of climate and circumstances is still more strongly marked in some of the tribes long settled in that region, whose descent may be traced to a distinct branch of the Syro-Arabian stock,

* See his "Varieties of Man," 1850, p. 469.

namely, the *Berber*, to which belong the Kabyles of Algiers and Tunis, the Tuaryks of Sahara, and the Guanches or ancient population of the Canary Isles. Amongst these tribes, whose affinity is indisputably traceable through their very remarkable language, every gradation may be seen, from the intense blackness of the Negro skin, to the more swarthy hue of the inhabitants of the South of Europe. It is remarkable that some of the Tuaryk inhabitants of particular Oases in the great desert, who are almost as insulated from communication with other races as are the inhabitants of islands in a wide ocean, have hair and features that approach those of the Negroes; although they speak the Berber language with such purity as to forbid the idea of the introduction of these characters by an intermixture of races. The *Jews*, who are the only remnants now existing of the once powerful Phœnician tribe, and who are now dispersed through nearly every country on the face of the earth, present a similar diversity; having gradually assimilated in physical characters to the nations among which they have so long resided (§ 787).

807. The second primary division of the Human family, according to the arrangement of Blumenbach, is that commonly termed *Mongolian*. The real Mongols, however, constitute but a single and not very considerable member of the group of nations accepted under this designation, which is, therefore, by no means an appropriate one. The original seat of these races appears to have been the great central elevated plain of Asia, in which all the great rivers of that continent have their sources, whatever may be their subsequent direction. Taken as a whole, this division is characterized by the pyramidal form of the skull, whose antero-posterior diameter scarcely exceeds the parietal, and by the broad flat face and prominent cheek-bones; by the flattening of the nose, which is neither arched nor aquiline; by the eyes being drawn upwards at their outer angle; by the xanthous or olive complexion, which sometimes becomes fair, but frequently swarthy; by the scantiness and straightness of the hair, and deficiency of beard; and by lowness of stature. These characters, however, are exhibited in a prominent degree only in the more typical members of the group, especially those inhabiting Northern and Central Asia; and may become so greatly modified, as to cease altogether to be recognizable. Such a modification has been remarkably effected in the case of a part of the *Turkish* people, now so extensively distributed. All the most learned writers on Asiatic history are agreed in opinion that the Turkish races are of one common stock; although at present they vary in physical characters, to such a degree that, in some, the original type has been altogether changed. Those which still inhabit the ancient abodes of the race, and preserve their pastoral nomadic life, present the physiognomy and general characteristics which appear to have belonged to the original Turkomans; and these are decidedly referable to the so-called Mongolian type. Before the Mahommedan era, however, the Western Turks or Osmanlis had adopted more settled habits, and had made considerable progress in civilization; and their adoption of the religion of Islam incited them to still wider extension, and developed that spirit of conquest, which, during the Middle Ages, displayed itself with such remarkable vigour. The branches of the race, which, from their long settlement in Europe, have made the greatest progress in civilization, now exhibit in all essential particulars the physical characters of the European model; and these are particularly apparent in the conformation of the skull.—Another marked departure from the ordinary Mongolian type is presented by the Hyperborean tribes inhabiting the borders of the Icy Sea; these have for the most part a pyramidal skull, but their complexion is swarthy and their growth is peculiarly stunted; and they form the link that

connects the ordinary Mongolidæ with the Lapps and Finns of Europe on one side, and with the Esquimaux of North America on the other. The Ugrian division, which migrated towards the north-west at a very early period, planted a colony in Europe, which still tenants the northern Baltic countries, forming the races of *Finns* and *Lapps*. In the time of Tacitus, the Finns were as savage as the Lapps; but the former, during the succeeding ages, became so far civilized as to exchange a nomadic life for one of agricultural pursuits, and have gradually assimilated with the surrounding people; whilst the Lapps, like the Siberian tribes of the same race, have ever since continued to be barbarous nomades, and have undergone no elevation in physical characters. The same division gave origin to the *Magyars* or Hungarians; a warlike and energetic people, unlike their kindred in the North; in whom a long abode in the centre of Europe has, in like manner, developed the more elevated characters, physical and mental, of the European nations.

808. The nations inhabiting the south-eastern and southern portions of Asia, also, appear to have had their origin in the Mongolian or Central-Asiatic stock; although their features and form of skull by no means exhibit its characteristic marks, but present such departures from it as are elsewhere observable in races that are making advances in civilization. The conformity of the Mongolian type is most decidedly shown by the nations (collectively termed *Seriform* by Dr. Latham) which inhabit China, Thibet, the Indo-Chinese peninsula, and the base of the Himalayan range; these are associated by certain linguistic peculiarities which distinguish them from all other races; that primitive condition of human speech, in which there is a total absence of inflections indicative of the relation of the principal words to one another, being apparently preserved with less change in the tongues of these people than in those of any other. The Chinese may be physically characterized as Mongolians softened down; and in passing from China towards India through the Burmese empire, there is so gradual a transition towards the ordinary Hindoo type, that no definite line of demarcation can be anywhere drawn. —The inhabitants of the great peninsula of Hindostan have been commonly ranked (as already remarked) under the Caucasian race; both on account of their physical conformity to that type, and also because it has been considered that the basis of their languages is Sanskritic. It is certain, however, that this conclusion is incorrect with regard to a very large proportion of the existing population of India; and there is strong reason to believe that no part of it bears any real relation of affinity to the Indo-European group of nations, except such as may be derived from a slight intermixture. Thus, the *Tamulian*, which is the dominant language of *Southern* India, is undoubtedly not Sanskritic in its origin (although containing an infusion of Sanskritic words), but more closely approximates to the Seriform type; and many of the hill tribes, in different parts of India, speak peculiar dialects, which, though mutually unintelligible, appear referable to the same stock. Now it is among this portion of the population of India that the greatest departure presents itself from the Caucasian type of cranial formation, and the closest conformity to the Mongolian; the cheek-bones being more prominent, the hair coarse, scanty, and straight, and the nose flattened; sometimes, also, the lips are very thick, and the jaws project, showing an approximation to the prognathous type. In the opinion of Dr. Latham and Mr. Norris, the various dialects of *Northern* India (of which the *Hindostani* is the most extensively spoken) are to be regarded as belonging, in virtue of their fundamental nature, to the same group with those of High Asia, notwithstanding the large infusion of Sanskritic words which they contain; this infusion having

been introduced at an early period by an invading branch of the Arian stock, of whose advent there is historical evidence, and whose descendants the ordinary Hindoo population have been erroneously supposed to be. According to this view, then, the influence of the Arian invasion upon the language and population of Northern India was very much akin to that of the Norman invasion upon those of England; the number of individuals of the invading race being so small in proportion to that of the indigenous population as to be speedily merged in it—not, however, without contributing to an elevation of its physical characters; and a large number of new words having been in like manner introduced, without any essential change in the type of the original language. And thus the only distinct traces of the Arian stock are to be found in the Brahminical caste, which preserves (though with great corruption) the original Brahminical religion, and which keeps up the Sanskrit as its classical language; it is certain, however, that this race is far from being of pure descent, having intermingled to a considerable extent with the ordinary Hindoo population. There is but little to remind us of the Mongolian type in the countenances of the Hindoos, which are often remarkable for a symmetrical beauty that only wants a more intellectual expression to render them extremely striking; some traces of it, however, may perhaps be found in the rather prominent zygomatic arches which are common amongst them; but the cranial portion of the skull presents no approach to the pyramidal type, being often very regularly elliptical. There is a remarkable difference in the colour of the different Hindoo tribes; some being nearly as dark as Negroes, others more of a copper colour, and others but little darker than the inhabitants of Southern Europe.*

809. According to the usual mode of dividing the Human family, the *Ethiopian* or *Negro* stock is made to include all the nations of Africa to the southward of the Atlas range. But, on the one hand, the Hottentots and Bushmen of the southern extremity constitute a group which is strongly distinguished by physical characters from the rest of the African nations; so, again, the region north of the Great Desert is mostly occupied by *Semitic* tribes (§ 806); the scattered population of the Great Desert itself is far from being Negro in many of its features; the valley of the Nile, at least in its middle and lower portions, including Egypt, Nubia, and even Abyssinia, is inhabited by a group of nations which may be designated as Nilotic, and which presents a series of gradational transitions between the Negroes and Kaffres and the Semitic races; a large portion of the area south of the Equator is occupied by the Kaffre tribes and their allies, which cannot be truly designated as Negroes; so that the true Negro area is limited to the western portion of the African continent, including the alluvial valleys of the Senegal, the Gambia, and the Niger, with a narrow strip of Central Africa, passing eastwards to the alluvial regions of the Upper Nile. Even within this area, the true Negro type of conformation, such as we see in the races which inhabit the low countries near the Slave Coast—consisting in the combination of the prognathous form of skull with receding forehead and depressed nose, thick lips, black woolly hair, jet-black unctuous skin, and crooked legs—is by no means universally prevalent; for many of the nations which inhabit it must be ranked as *sub-typical* Negroes; and from these the gradation in physical characters is by no means abrupt, to those African nations which possess, in a considerable degree, the attributes which we are accustomed to exclude

* For many interesting particulars respecting the physical characters and habits of the wild tribes of the Veddahs of Ceylon, see a Paper by J. Bailey in the "Transactions of the Ethnological Society," vol. ii. p. 278.

altogether from our idea of the African race. Thus, the race of Jolofs near the Senegal, and the Guber in the anterior of Sudan, have woolly hair and deep-black complexions, but fine forms and regular features of a European cast; and nearly the same may be said of the darkest of the Kaffres of Southern Africa. The Bechuana Kaffres present a still nearer approach to the European type; the complexion being of a light-brown, the hair often not woolly but merely curled, or even in long-flowing ringlets, and the figure and features having much of the European character.—There is no group, in fact, which presents a more constant correspondence between external conditions and physical conformation, than that composed of the African nations. As we find the complexion becoming gradually darker, in passing from Northern to Southern Europe, thence to North Africa, thence to the borders of the Great Desert, and thence to the intertropical region where alone the dullest black is to be met with—so do we find, on passing southwards from this, that the hue becomes gradually lighter in proportion as we proceed farther from the equator, until we meet with races of comparatively fair complexions among the nations of Southern Africa. Even in the intertropical region, high elevations of the surface have the same effect as we have seen them to produce elsewhere, in lightening the complexion. Thus, the high parts of Senegambia, where the temperature is moderate and even cool at times, are inhabited by Fulahs of a light copper colour, whilst the nations inhabiting the lower regions around them are of true Negro blackness: and nearly on the same parallel, but at the opposite side of Africa, are the high plains of Enarea and Kaffa, of which the inhabitants are said to be fairer than the natives of Southern Europe.

810. The languages of the Negro nations, so far as they are known, appear to belong to one group, for although there is a considerable diversity in their vocabularies (arising in great part from the want of written records which would give fixity to their tongues), yet they seem to present the same grade of development and the same grammatical forms; and various proofs of their affinity with the Semitic languages have been developed, these being afforded by similarity alike of roots and of grammatical construction. The Semitic affinity of the Negro nations is farther indicated in a very remarkable manner, by the existence of a variety of superstitions and usages among the Negroes of the Western Coast, closely resembling those which prevail also among the Nilotic races whose Semitic relations are most clear, as well as among branches of the Semitic stock itself; and thus we seem to have adequate proof of the absence of any definite line of demarcation, in regard either to *physiological* or to *linguistic* characters between the Negro race, and one of those which has been hitherto considered to rank among the most elevated forms of the Caucasian variety.—Nor is there anything in the *psychical* character of the Negro which gives us a right to separate him from other races of mankind. It is true that those races which have the Negro character in an exaggerated degree are uniformly in the lowest stage of society, being either ferocious savages, or stupid, sensual, and indolent; such are most of the tribes along the Slave Coast. But, on the other hand, there are many Negro States, the inhabitants of which have attained a considerable degree of improvement in their social condition; such are the Ashanti, the Sulima, and the Dahomans of Western Africa, also the Guber of Central Sudan, among which a considerable degree of civilization has long existed; the physical characters of all these nations deviate considerably from the strongly-marked or exaggerated type of the Negro; and the last are perhaps the finest race of genuine Negroes on the whole continent, and present in their language the most distinct traces of

original relationship to the Syro-Arabian nations. The highest civilization, and the greatest improvement in physical characters, are to be found in those African nations which have adopted the Mahommedan religion; this was introduced, three or four centuries since, into the eastern portion of Central Africa; and it appears that the same people, which were then existing in the savage condition still exhibited by the Pagan nations farther south, have now adopted many of the arts and institutions of civilized society, subjecting themselves to governments, practising agriculture, and dwelling in towns of considerable extent, many of which contain 10,000, and some even 30,000 inhabitants; a circumstance which implies a considerable advancement in industry, and in the resources of subsistence. This last fact affords most striking evidence of the *improvability* of the Negro races; and, taken in connection with the many instances that have presented themselves, of the advance of individuals, under favourable circumstances, to at least the average degree of mental development among the European nations, it affords clear proof that the line of demarcation, which has been supposed to separate them intellectually and morally from the races that have attained the greatest elevation, has no more *real* existence than that which has been supposed to be justified by a difference in physical characters, and of which the fallacy has been previously demonstrated (§ 802).

811. The southern portion of the African continent is inhabited by a group of nations, which (as already mentioned) recede more or less decidedly from the Negro type in physical characters, and which seem connected together by essential community of language, as branches of the stock of which the *Kaffres* may be considered the stem. In this warlike nomadic people, which inhabit the eastern parts of South Africa, to the northward of the Hottentot country, so great a departure from the ordinary Negro type presents itself, that many travellers have assigned to them a different origin. The degree of this departure, however, varies greatly in the different Kaffre tribes; for whilst some of them are black, woolly-headed, and decidedly prognathous, so as obviously to approach the modified Negroes of Congo in general aspect, others recede considerably from the typical prognathous races, both in complexion, features, and form of head, presenting a light-brown colour, a high forehead, a prominent nose, and a tall, robust, well-shaped figure. The thick lips and black frizzled hair, however, are generally retained; though the hair is sometimes of a reddish colour, and becomes flowing; and the features may present a European cast. But even among the tribes which depart most widely from the Negro type, individuals are found who present a return to it; and it is interesting to remark, that the people of Delagoa Bay, though of the Kaffre race (as indicated by their language), having been degraded by subjugation, approach the people of the Guinea Coast in their physical characters. In fact, between the most elevated Kaffre and the most degraded Negro every possible gradation of physical and psychical characters is presented to us, as we pass northward and westwards from Kaffraria towards the Guinea Coast; and we meet with a similar transition, although not carried to so great an extent, as we pass up the eastern coast.—The languages of the Kaffres and other allied tribes are distinguished by a set of remarkable characters, which have been considered as isolating them from other African tongues. According to Dr. Latham, however, these peculiarities are not so far without precedent elsewhere as to establish the very decided line of demarcation which some have attempted to draw; and may be regarded, in fact, as resulting from the fuller development of tendencies which manifest themselves in other African languages.

812. The *Hottentot* race differs from all other South African nations both in language and in physical conformation. Its language cannot be shown to possess distinct affinities with any other stock;* but in bodily structure there is a remarkable admixture of the characters of the Mongolian with those of the Negro. Thus, the face presents the very wide and high cheek-bones, with the oblique eyes and flat nose of the Northern Asiatics; at the same time that, in the somewhat prominent muzzle and thick lips, it resembles the countenance of the Negro. The complexion is of a tawny buff or fawn colour, like the black of the Negroes diluted with the olive of the Mongols. The hair is woolly, like that of the Negroes, but it grows in small tufts scattered over the surface of the scalp (like a scrubbing-brush), instead of covering it uniformly: thus resembling in its comparative scantiness that of the Northern Asiatics. It is most interesting to observe this remarkable resemblance in physical characters, between the Hottentots and the Mongolian races, in connection with the similarity that exists between the circumstances under which they respectively live; and it is not a little curious that the Hottentot, as the Mongol, should be distinguished by the extraordinary acuteness of his vision. No two countries can be more similar than the vast steppes of Central Asia and the karroos of Southern Africa; and the proper inhabitants of each are nomadic races, wandering through deserts remarkable for the wide expansion of their surface, their scanty herbage, and the dryness of their atmosphere, and feeding upon the milk and flesh of their horses and cattle. Of the original pastoral Hottentots, however, comparatively few now remain. A large proportion of them have been gradually driven, by the encroachments of the Kaffres and of European colonists, and by internal wars with each other, to seek refuge among the inaccessible rocks and deserts of the interior; and have thus been converted from a mild, unenterprising race of shepherds, into wandering hordes of fierce, suspicious, and vindictive savages, treated as wild beasts by their fellow-men, until they become really assimilated to wild beasts in their habits and dispositions. Hence have arisen the tribes of *Bushmen* or *Bosjesmen*, which are generally regarded as presenting the most degraded and miserable condition of which the Human race is capable, and have been supposed (but erroneously) to present resemblances in physical characters to the higher Quadrumana. This transformation has taken place, under the observation of eye-witnesses, in the Koranas, a tribe of Hottentots well-known to have been previously the most advanced in all the improvements which belong to pastoral life; for having been plundered by their neighbours, and driven out into the wilderness to subsist upon wild fruits, they have adopted the habits of the Bushmen, and have become assimilated in every essential particular to that miserable tribe.—It appears, however, from the inquiries of Dr. Andrew Smith, that this process of degradation has been in operation quite independently of external agencies; nearly all the South African tribes who have made any advances in civilization being surrounded by more barbarous hordes, whose abodes are in the wilderness of

* It is considered by some, that the Hottentot language is a degraded Kaffre, as the Bushman language is a degraded Hottentot; but the Author is informed by Mr. Norris that he sees no valid ground for this assumption; the affinities of the Hottentot language being rather, in his opinion, with the languages of High Asia, although the connecting links are extremely slight. Such as they are, however, they tend to confirm an idea suggested to the Author some years since by the marked reproduction of so many Mongolian characters in the Hottentot race—that it is the remnant of a migration from Asia, earlier than that in which the great bulk of the African nations have their origin; and that it has been driven down to the remotest corner of the Continent, just as the aboriginal (Mongolian) population of south-western Europe seems to have been driven back by the Indo-European immigration (§ 805).

mountains and forests, and who constantly recruit their numbers by such fugitives as crime and destitution may have driven from their own more honest and more thriving communities; and these people vary their mode of speech designedly, and even adopt new words, in order to make their meaning unintelligible to all but the members of their association. This has its complete parallel in the very midst of our own or any other highly civilized community; all our large towns containing spots nearly as inaccessible to those unacquainted with them, as are the rude caves or clefts of hills, or the burrows scooped out of the level karroo, in which the wretched Bushman lies in wait for his prey; and these being tenanted by a people that have been well characterized as *les classes dangereuses*, which, as often as the arm of the law is paralyzed, issue forth from the unknown deserts within which they lurk, and rival in their fierce indulgence of the most degrading passions, and in their excesses of wanton cruelty, the most terrible exhibitions of barbarian inhumanity. Such outcasts, in all nations, purposely adopt, like the Bushmen, a 'flash' language; and in their general character and usages there is a most striking parallel.*

813. The *American* nations, taken collectively, form a group which appears to have existed as a separate family of nations from a very early period in the world's history. They do not form, however, so distinct a variety, in regard to physical characters, as some anatomists have endeavoured to prove; for, although certain peculiarities have been stated to exist in the skulls of the aboriginal Americans, yet it is found, on a more extensive examination, that these peculiarities are very limited in their extent—the several nations spread over this vast continent differing from each other in physical peculiarities as much as they do from those of the Old World, so that no typical form can be made out among them. In regard to complexion, again, it may be remarked, that although the native Americans have been commonly characterized as "red men," they are by no means invariably of a red or coppery hue, some being as fair as many European nations, others being yellow or brown, and others nearly, if not quite, as black as the Negroes of Africa; whilst, on the other hand, there are tribes equally red, and perhaps more deserving that epithet, in Africa and Polynesia. Our ordinary notion of the American races, having been chiefly founded upon the characters of those tribes of 'Indians' with whom European settlers first came into contact, proves to be no more applicable to the inhabitants of the Continent generally, than are the characters of the Negro to the population of Africa as a whole (§ 809).—In spite of all this diversity of conformation, it is believed that the structure of their languages affords a decided and clearly-marked evidence of relationship between them (§ 805). Notwithstanding their diversities in mode of life, too, there are peculiarities of mental character, as well as a number of ideas and customs derived from tradition, which seem to be common to them all; and which for the most part indicate a former elevation in the scale of civilization, that has left its traces among them even in their present depressed condition, and still distinguishes them from the sensual, volatile, and almost animalized savages that are to be met with in many parts of the Old Continent. —The Esquimaux have been regarded as constituting an exception to all general accounts of the physical characters of the American nations; for in the configuration of their skulls, as also in their complexion and general physiognomy, they conform to the Mongolian type, even presenting it in an exaggerated degree; whilst their wide extension along the whole northern coast of America, through the Aleutian Islands, and even to the Continent of

* See "London Labour and the London Poor," p. 2.

Asia, certainly lends weight to the idea that they derive their origin from the Northern Asiatic stock. But the increased acquaintance which has been recently gained with the tribes that people the north-eastern portion of the American Continent, has clearly shown that no physical separation can be established between the Esquimaux and the Indian proper; the one form graduating so insensibly into the other, as to make the distinction between the two groups there as difficult as on the western side it is easy. Hence the existence of the Esquimaux population in this situation affords a complete link of transition between the Asiatic and the American nations, in the precise region in which the geographical relations of the two continents would lead us to expect it.

814. It now remains for us to notice the *Oceanic* races which inhabit the vast series of islands scattered through the great ocean that stretches from Madagascar to Easter Island. There is no part of the world which affords a greater variety of local conditions than this, or which more evidently exhibits the effects of physical agencies on the organization of the human body. Moreover, it affords a case for the recognition of affinities by means of language that possesses unusual stability; since the insulated position of the various tribes that people the remote spots of this extensive tract prevents them from exercising that influence upon each other's forms of speech which is to be observed in the case of nations united by local proximity or by frequent intercourse. Tried by this test, it is found that the different groups of people inhabiting the greater part of these insular regions, although so widely scattered and so diverse in physical characters, are more nearly connected together than most of the families of men occupying continuous tracts of land on the great continents of the globe. A probable explanation of this remarkable affinity has been afforded by the careful investigation of the Flora and Fauna of those regions* by Sir Joseph Hooker and Mr. Wallace; whose observations furnish strong evidence that most important and extensive geological changes have taken place since the islands scattered over that region have been peopled by their existing inhabitants. The western and eastern halves of the Indian archipelago, the former containing Sumatra and Borneo, the latter including Celebes and New Guinea, are separated at their nearest approximation by the Straits of Lombok, which are no more than fifteen miles wide: the Fauna of the former is essentially Asiatic, that of the latter essentially Australian; and there is no other intermixture between them than such as a very limited migration across this narrow channel will readily account for. Now the various portions of the Indian province are still connected by a vast submarine plain, which extends over the whole of the Java Sea, the Straits of Malacca, the Gulf of Siam, and the southern part of the China Sea, at a depth of not more than three hundred feet, abruptly terminating at its limits in an unfathomable ocean. An elevation of the sea-bottom to this amount, therefore, would nearly double the extent of tropical Asia; and there is every probability that the Continent *was* thus extended before that last great elevation of the volcanic range of Java and Sumatra took place, which (according to the general fact first brought into notice by Dr. Darwin, of an alternation of bands of elevation and depression) was coincident with the subsidence that separated those islands from Borneo on the one side and

* See the "Introductory Essay to the Flora of New Zealand," by Sir J. D. Hooker, 1853, and his "Flora of Australia; its Origin, Affinities, and Distribution," 1859. Also Mr. A. R. Wallace, 'On the Zoological Geography of the Malay Archipelago,' in the "Proceedings of the Linnæan Society" for November, 1859; and the Review of these works in the "Medico-Chir. Rev." for 1860, vol. xxv. p. 371, as well as his more recent work on "Geographical Distribution."

from the continent of Asia on the other. On the other hand, the great Pacific Continent, of which New Guinea and Australia are doubtless fragments, and which (as Sir Joseph Hooker has rendered probable by botanical and Wallace* by zoological considerations) once connected Australia and New Zealand with South America, seems to have extended itself as far westward as the Moluccas; and *its* submergence, producing the limitation and separation of the great islands of the South Sea, seems to have taken place before the rise of the tropical Asiatic continent. There are even indications that the tropical Indian Continent extended so near to what is now the coast of Africa, that the Isle of Bourbon and the Mauritius, perhaps even Madagascar, were outlying portions of it; and if the submergence which formed the bed of the present Indian Ocean should have taken place subsequently to the time when those countries became inhabited by Man, we have a rational explanation of the fact which has perplexed all ethnologists, and which the hypothesis of migration can scarcely be stretched far enough to account for—that both the Fauna and the languages of Madagascar are rather Malayo-Polynesian than African in their fundamental affinities.

815. The inhabitants of Oceania seem divisible into two principal groups, which are probably to be regarded as having constituted distinct races from a very early period; these are, the Malayo-Polynesian race, and the Negritos or Pelagian Negroes. The *Malayo-Polynesian* group is by far the more extensive of the two; and comprehends the inhabitants of the greater part of the Indian and Polynesian Archipelagoes, with the peninsula of Malacca (which is the centre of the Malays proper), and perhaps the inhabitants of Madagascar. These are all closely united by affinities of language. The proper Malays bear a strong general resemblance to the Mongolian races, and this resemblance is shared, in a greater or less degree, by most of the inhabitants of the Indian Archipelago. They are of a darker complexion, as might be expected from their proximity to the equator; but in this complexion yellow is still a large ingredient. The Polynesian branch of the group presents a much wider diversity; and if it were not for the community of language, it might be thought to consist of several races as distinct from each other as from the Malayan branch. Thus the Tahitians and Marquesans are tall and well-made; their figures combine grace and vigour; their skulls are usually remarkably symmetrical; and their physiognomy presents much of the European cast, with a very slight admixture of the features of the Negro. The complexion, especially in the females of the higher classes who are sheltered from the wind and sun, is of a clear olive or brunette, such as is common among the natives of Central and Southern Europe; and the hair, though generally black, is sometimes brown or auburn, or even red or flaxen. Among other tribes, as the New Zealanders and the Tonga and Friendly Islanders, there are greater diversities of conformation and hue; some being finely proportioned and vigorous, others comparatively small and feeble; some being of a copper-brown colour, others nearly black, and others again almost white. In fact, if we once admit a strongly-marked difference in complexion, features, hair, and general configuration, as establishing a claim to original distinctness of origin, we must admit the application of this hypothesis to almost every group of islands in the Pacific—an idea, of which the essential community of language seems to afford a sufficient refutation. Among the inhabitants of Madagascar, too, all of which speak dialects of the same language, some bear a strong resemblance to those of the Malayan type, whilst others present approaches to that of the Negro.

* A. R. Wallace, "Geographical Distribution of Animals," vol. i. 1876, p. 387.

816. The *Negrito* or *Pelagian-Negro* races must be regarded as a group altogether distinct from the preceding; having a marked diversity of language; and presenting, more decidedly than any of the Malayo-Polynesians, the characters of the Negro type. They form the predominating population of New Britain, New Ireland, the Louisiade and Solomon Isles, of several of the New Hebrides, and of New Caledonia; and they seem to extend westwards into the mountainous interior of the Malayan Peninsula, and into the Andaman Islands in the Bay of Bengal.* The Tasmanians, or aborigines of Van Diemen's Land, who are now almost completely exterminated, undoubtedly belonged to this group. Very little is known of them, except through the reports of the people of Malayo-Polynesian race inhabiting the same islands; but it appears that, generally speaking, they have a very inferior physical development, and lead a savage and degraded life. There is considerable diversity of physical characters among them; some approximating closely in hair, complexion, and features, to the Guinea-Coast Negroes; whilst others are of yellower tint, straight hair, and better general development. The *Papuans*, who inhabit the northern coast of New Guinea and some adjacent islands, and who are remarkable for their large bushy masses of half-woolly hair, have been supposed to constitute a distinct race; but there is little doubt that they are of hybrid descent, between the Malays and the Pelagian Negroes.—To this group we are probably to refer the *Alfourous* or *Alforian* race, which are considered by some to be the earliest inhabitants of the greater part of the Malayan Archipelago, and to have been supplanted by the more powerful people of the preceding races, who have either extirpated them altogether, or have driven them from the coasts into the mountainous and desert parts of the interior. They are yet to be found in the central parts of the Moluccas and Philippines; and they seem to occupy most of the interior and southern portion of New Guinea, where they are termed Endamenes. They are of very dark complexion; but their hair, though black and thick, is lank. They have a peculiarly repulsive physiognomy; the nose is flattened, so as to give the nostrils an almost transverse position; the cheek-bones project; the eyes are large, the teeth prominent, the lips thick, and the mouth wide. The limbs are long, slender, and misshapen. From the close resemblance in physical characters between the Endamenes of New Guinea and the aborigines of New Holland, and from the proximity between the adjacent coasts of these two islands, it may be surmised that the latter belong to the Alforian race; but too little is known of the language of either to give this inference a sufficient stability. In the degradation of their condition and manner of life, the savages of New Holland fully equal the Bushmen of South Africa; and it is scarcely possible to imagine human beings existing in a condition more nearly resembling that of brutes. But there is reason to believe, that the tribes in closest contact with European settlers are more miserable and savage than those of the interior; and even with respect to these, increasing acquaintance with their language, and a consequent improved insight into their modes

* An interesting paper 'On the Mincopie Race of the Andaman Isles,' by Professor Owen, will be found in the "Transactions of the Ethnological Society" for 1863, p. 34. They appear to be amongst the most degraded of the Human species, possessing no notion of a Supreme Being, nor of a future existence, nor any sense of decency or shame; they are of diminutive size, yet the cranium is well formed, of an oval type, with rather receding forehead, and they are skilful in making knives of glass and iron cast up from wrecks. They possess considerable powers of imitation, and are active in running, climbing, and swimming. They are not cannibals. Prof. Owen concludes that they are the aborigines of these islands, but remarks that antecedent generations may have coexisted with the slow and gradual geological changes which have obliterated the place or continent of their primitive origin. See also a Paper on 'The Admiralty Islanders,' by H. N. Moseley, "Trans. Anthrop. Soc.," 1877.

of thought, tend to raise the very low estimate which has been formed and long maintained in regard to their extreme mental degradation. The latest and most authentic statements enable us to recognize among them the same principles of a moral and intellectual nature, which, in more cultivated tribes, constitute the highest endowments of humanity; and thus to show that they are not separated by any impassable barrier from the most civilized and elevated nations of the globe.—There are many indications, indeed, that the Negrito race is not so radically distinct from the Malayo-Polynesian as the marked physical dissimilarity of their respective types, and the apparent want of conformity between their languages, would make it appear. For as, on the one hand, some of the subdivisions of the latter present a decided tendency towards that prognathous character and depth of complexion which are typical of the former, so among the former do we not unfrequently meet with a lighter shade of skin, a greater symmetry of skull, and a considerable improvement in form and feature. And although no very close relationship can be discovered between the Negrito and Malayo-Polynesian languages, yet it has been pointed out by Mr. Norris that a much more decided relationship exists between the Australian and the Tamulian (§ 808); and remote as this connection seems, the circumstance adds weight to the idea, that the native Australians (with other Negrito tribes) are an off-set from that southern branch of the great nomadic stock of Central Asia, which seems early to have spread itself through the Indo-Chinese and the Indian Peninsulas, and to have even there shown an approximation to the prognathous type.

817. Looking, then, to the great diversity which exists among the subordinate groups of which both these divisions consist, and their tendency to mutual approximation, it cannot be shown that any sufficient reason exists for isolating them from each other; and, as already remarked (§ 815), there seems no medium between the supposition that each island had its aboriginal pair or pairs, and the doctrine that the whole of Oceania has been peopled from a common stock. Looking, again, to the very decided approximation which is presented by certain Oceanic tribes to the Mongolian type, and this in localities which, on other grounds, might be regarded as having received the first stream of migration, the possibility, to say the least, can scarcely be denied, that the mainland furnished the original stock, which has undergone various transformations subsequently to its first dispersion; these having been the result of climatic influence and mode of life, and having been chiefly influenced as to degree by the length of time during which the transforming causes have been in operation. At any rate, it may be safely affirmed, that the Oceanic races are not entitled by any distinctive physical peculiarity to rank as a group which must have necessarily had an original stock distinct from that of the Continental nations.

CHAPTER XX.

OF THE MODES OF VITAL ACTIVITY CHARACTERISTIC OF DIFFERENT AGES.

818. Although from the time when the Human being comes into the world, to the final cessation of his corporeal existence, the various functional operations of Organic life are carried on with ceaseless activity, whilst those of Animal life are only suspended by the intervals of repose which are needed for the renovation of their organs, yet there are very marked differences, not

only in the *degree of their united activity*, but also in the *relative degrees of energy which they severally manifest*, at different epochs. These differences, taken in connection with the modifications in the size and conformation of the body with which they are in relation, mark out the whole term of life into the various 'Ages,' which are commonly recognized as seven—namely, Infancy, Childhood, Youth, Adolescence, Manhood, Decline, and Senility. For Physiological purposes, however, a less minute subdivision is equally or perhaps more appropriate—namely, the three great periods of *Growth and Development*, of *Maturity*, and of *Decline*. The first comprehends the whole of that series of operations by which the germ evolves itself at the expense of the nutriment which it appropriates from external sources into the complete organism, possessed not merely of its full dimensions, but of its highest capacity for every kind of functional activity; this includes, therefore, the epochs of Embryonic life, Infancy, Childhood, Youth, and Adolescence, all of which are characterized by an *excess* of the *constructive* over the *destructive* changes taking place in the organism. The second period ranges over the whole term of Manhood, in which the organism, having attained its complete development, is brought into vigorous and sustained activity; and in which it is *maintained* in a condition fitted for such activity, by the equilibrium which subsists between the operations of redintegration and of disintegration. The third period commences with the incipient failure of the bodily powers, consequent upon the *diminished* activity of the *constructive* powers, as compared with that of the changes which involve *degeneration* and *decay;* this diminution begins to manifest itself during the latter part of Middle Life, before Old Age can properly be said to commence; and it continues in an increasing ratio through the whole 'decline of life,' until the reparative powers being exhausted, Death supervenes as the necessary termination of that long succession of phenomena of which Life consists.

819. Although the organization of the body at each epoch may be truly said to be the *resultant* of all the *material* changes which it has undergone during the preceding periods, yet it is scarcely possible to take an enlarged view of the case, without perceiving that we must look for the cause of this succession in those *dynamical* conditions, the presence of which is the distinguishing attribute of living structures. Every *constructive* act, whether this consist in Growth (§ 309) or in Development (§ 310), not merely requires *materials* for the new tissue produced, but depends upon the active operation of a *formative power*, without whose agency these materials would remain unorganized. In our examination into the source of the formative power which we see thus operating in every individual organism (CHAP. I.), we found it traceable to the *Physical* Forces to which it is subjected (Heat being the one which seems to bear most directly upon the formative operations); these forces being metamorphosed, so to speak, into the constructive force of the living body, in virtue of the peculiar endowments of *its* material substratum—just as an Electric current transmitted through the different nerves of Sense produces the sensory impressions which are characteristic of each respectively (§ 426); or as the same current, transmitted through one form of Inorganic matter, produces Light and Heat, through another, Chemical Change, or through another, Magnetism. But we must also recognize in the Organism at large, as well as in every integral part of it, a certain *capacity* for growth and development—which is the original endowment of its *germ*—which not only determines the mode in which it shall progressively evolve itself into the fabric characteristic of its species and sex, but also shapes the peculiarities of the individual—which serves also to bring about the per-

petual reconstruction that is needed for its continued maintenance, and is peculiarly manifested in those reparative processes which make good losses of its substance resulting from injury or disease—and of which the cessation, by preventing any further metamorphoses of Physical into Vital force, causes the constructive powers to fail altogether, so that the Organism is resolved back by these very forces into the various forms of Inorganic matter at the expense of which it had been built up.

820. Now this 'general capacity' is most strikingly displayed during those earliest periods of existence, in which growth and development alike are taking place most rapidly; in fact, the farther we go back in the history of intra-uterine life, the more energetic do we perceive its manifestations to be. For when we look simply at the *increase* from the minute point that constitutes the first perceptible germ, to the mature fœtus of 6 or 7 lbs. weight, we see that at no other period of existence can that increase be compared in its rate with that which presents itself during the nine months that follow conception; and if we go more into detail, we find that it is yet more remarkable in the earlier than in the later months (§ 822). So, again, it is in the first few weeks of embryonic life that the foundation is laid of most of its permanent *organs*, in the midst of an apparently homogeneous mass of cells; whilst in the succeeding weeks these rudiments are evolved into the semblance of the forms they are subsequently to present, and a differentiation of *tissues* begins to show itself in their several parts; so that the developmental process is so far advanced at little more than half the term of gestation, that the fœtus may even then, under favourable circumstances, maintain an independent existence (§ 722). The rate of increase becomes progressively slower during the advance from infancy to maturity; and the energy of the developmental process is comparatively enfeebled, being limited to the perfecting of structures whose foundations had been previously laid, and in no instance manifesting itself normally in the evolution of a new part or organ. Now as there is no limit (in the well-nourished individual) to the supply of Food and Warmth, it follows that this gradual decline of formative activity must be due to a diminution of the *capacity* for that activity, inherent in the organism itself; and this diminution is still more strongly marked by that entire cessation, both of increase, and of further developmental changes, which constitutes the termination of the first period. For the organism which has attained that stage of its existence has so far lost the formative capacity which characterized its earlier years, that, however copious the supply of food, however abundant the generation of heat, it can thenceforth do no more than *maintain* its normal condition, and can effect this for only a limited term of years. It seems a necessary sequence of this series of phenomena, that the time should come, when, after a period of gradual decline, the germinal capacity of the organism should be so much reduced as no longer to suffice for the maintenance of its own integrity; and whenever such is the case, the termination of its existence as a living body must be the necessary result. Hence we find that there is a natural limit, not only to the size and development of the organism, but also to the duration of its life. And although that limit in each case is subject to variation amongst *individuals*, partly in consequence of diversity of external conditions, but partly (it may be surmised) through differences in the measure of germinal capacity possessed by each, yet there is a limit also to these variations, so that the character of the *species* is never departed from.

821. *Period of Growth and Development.*—The general history of the first part of this period, that of Embryonic existence, has already been so fully given, that it is only necessary here to remark briefly in regard to the charac-

ter of its vital operations, that the whole nisus of its activity is directed rather to the performance of the *vegetative* or *organic* than to that of the *animal* functions; the action of the heart, and the occasional reflex movements of the limbs, being its only manifestations of nervo-muscular power. And thus it seems to be that the formative capacity is greater during embryonic life, than at any subsequent period, and greater in its earlier than its later stages; so that we have not only evidence of an extraordinary power of regenerating parts which have been lost by disease or accident, as seen in attempts at the reproduction of entire limbs after their 'spontaneous amputation' (§ 337); but there is also not unfrequently an absolute excess of productive power, as shown in the development of supernumerary organs, which may even proceed to the extent of the complete duplication of the entire body, by the early subdivision of the embryonic structure into two independent halves.—It is to be noticed, also, that the embryo derives its supply not merely of food, but also of *heat*, from its maternal parent; and it is probably owing especially to the constancy with which this force operates, that the period of embryonic development is so uniform in Man (as in warm-blooded Animals generally), by comparison with the corresponding developmental periods in Plants and cold-blooded Animals, these being entirely determined by the degree of heat to which the embryos are subjected.

822. It is frequently of great importance, both to the Practitioner and to to the Medical Jurist, to be able to determine the *age* of a Fœtus from the physical characters which it presents; and the following Table has been framed by Devergie* in order to facilitate such determination. It is to be remarked, however, that the *absolute length* and *weight* of the Embryo are much less safe criteria than its *degree of development*, as indicated by the relative evolution of the several parts which make their appearance successively. Thus it is very possible for one child born at the full time, to *weigh* less than another born at 8 or even at 7 months; its *length*, too, may be inferior; and even the position of the *middle point* of the body is not, taken alone, a safe criterion, since it is liable to variation in individuals.†

Embryo 3 *to* 4 *weeks*.—It has the form of a serpent;—its length from 3 to 5 lines;—its head indicated by a swelling;—its caudal extremity (in which is seen a white line, indicating the continuation of the medulla spinalis), slender, and terminating in the umbilical cord;—the mouth indicated by a cleft, the eyes by two black points;—members begin to appear as nipple-like protuberances;—liver occupies the whole abdomen;—the bladder is very large;—the chorion is villous, but its villosities are still diffused over the whole surface.

Embryo of 6 *weeks*.—Its length from 7 to 10 lines;—its weight from 40 to 75 grains;—face distinct from cranium;—aperture of nose, mouth, eyes and ears perceptible;—head distinct from thorax;—hands and fore-arms in the middle of the length; fingers distinct;—legs and feet situated near the anus;—clavicle and maxillary bone present a point of ossification;—distinct umbilicus for attachment of cord, which at that time consists of the omphalo-mesaraic vessels, of a portion of the urachus, of a part of the intestinal tube, and of filaments which represent the umbilical vessels;—the placenta begins to be formed; the chorion still separated from the amnion;—the umbilical vesicle very large.

Embryo of 2 *months*.—Length from 16 to 19 lines; weight from 150 to 300 grains;—elbows and arms detached from the trunk;—heels and knees also isolated;—rudiments of the nose and of the lips;—palpebral circle beginning to show itself;—clitoris or penis apparent;—anus marked by a dark spot;—rudiments of lungs, spleen, and suprarenal capsules;—cæcum placed behind the umbilicus;—digestive canal withdrawn into the abdomen;—urachus visible;—osseous points in the frontal bone and in the ribs;—chorion commencing to touch the amnion at the point opposite the insertion of the placenta;—placenta begins to assume its regular form;—umbilical vessels commence twisting.

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* "Médecine Légale," 3ème édit.; tom. i. p. 279.

† See, on this last point, Moreau in "Lancette Française," 1837; and Dr. A. Taylor in "Guy's Hospital Reports," 1842.

Embryo of 3 months.—Length from 2 to 2½ inches;—weight from 1 oz. to 1½ oz. (Troy)—head voluminous:—eyelids in contact by their free margin;—membrana pupillaris visible;—mouth closed;—fingers completely separated;—inferior extremities of greater length than rudimentary tail;—clitoris and penis very long;—thymus as well as suprarenal capsules present;—cæcum placed below the umbilicus;—cerebrum 5 lines, cerebellum 4 lines;—medulla oblongata 1½ line, and medulla spinalis ¾ of a line in diameter;—two ventricles of heart distinct;—the decidua reflexa and decidua uterina in contact;—funis contains umbilical vessels and a little of the gelatin of Wharton;—placenta completely isolated;—umbilical vesicle, allantois, and omphalo-mesaraic vessels have disappeared.

Fœtus of 4 months.—Length 5 to 6 inches;—weight 2½ to 3 oz.; skin rosy, tolerably dense;—mouth very large and open;—membrana pupillaris very evident;—nails begin to appear;—genital organs and sex distinct;—cæcum placed near the right kidney;—gall-bladder appearing;—meconium in duodenum;—cæcal valve visible;—umbilicus placed near pubis;—ossicula auditûs ossified;—points of ossification in superior part of sacrum;—membrane forming at point of insertion of placenta on uterus;—complete contact of chorion with amnion.

Fœtus of 5 months.—Length 6 to 7 inches;—weight 5 to 7 oz.;—volume of head still comparatively great;—nails very distinct;—hair beginning to appear;—skin without sebaceous covering;—white substance in cerebellum;—heart and kidneys very voluminous;—cœcum situated at inferior part of right kidney;—gall-bladder distinct;—germs of permanent teeth appear;—points of ossification in pubis and calcaneum;—meconium has a yellowish green tint, and occupies commencement of large intestine.

Fœtus of 6 months.—Length 9 to 10 inches;—weight 1 lb.;—skin presents some appearance of fibrous structure;—eyelids still agglutinated, and membrana pupillaris remains;—sacculi begin to appear in colon;—funis inserted a little above pubis;—face of a purplish red;—hair white or silvery;—sebaceous covering begins to present itself;—meconium in large intestine;—liver dark-red; gall-bladder contains serous fluid destitute of bitterness;—testes near kidneys;—points of ossification in four divisions of sternum;—middle point at lower end of sternum.

Fœtus of 7 months.—Length 13 to 15 inches;—weight 3 to 4 lbs.;—skin of rosy hue, thick, and fibrous;—sebaceous covering begins to appear;—nails do not yet reach extremities of fingers;—eyelids no longer adherent;—membrana pupillaris disappearing;—a point of ossification in the astragalus;—meconium occupies nearly the whole of the large intestine;—valvulæ conniventes begin to appear;—cæcum placed in right iliac fossa;—left lobe of liver almost as large as right;—gall-bladder contains bile;—brain posssesses more consistency;—testicles more distinct from kidneys;—middle point at a little below end of sternum.

Fœtus of 8 months.—Length 14 to 16 inches;—weight 4 or 5 lbs.;—skin covered with well-marked sebaceous envelope;—nails reach extremities of fingers;—membrana pupillaris becomes invisible during this month;—a point of ossification in the last vertebra of sacrum;—cartilage of inferior extremity of femur presents no centre of ossification;—brain has some indications of convolutions;—testicles descend into inguinal ring;—middle point nearer the umbilicus than the sternum.

Fœtus of 9 months, the full term.—Length from 17 to 21 inches;—weight from 5 to 9 lbs., the average probably about 6½ lbs;—head covered with hair in greater or less quantity, of from 9 to 12 lines in length;—skin covered with sebaceous matter, especially at bends of joints;—membrana pupillaris no longer exists;—external auditory meatus still cartilaginous;—four portions of occipital bone remain distinct;—os hyoides not yet ossified;—point of ossification in the centre of cartilage at lower extremity of femur;—white and grey substances of brain become distinct;—liver descends to umbilicus;—testes have passed inguinal ring, and are frequently found in the scrotum;—meconium at termination of large intestine;—middle point of body at umbilicus, or a little below it.

823. From the time of its entrance into the world, the condition of the Human infant is essentially changed. It is no longer supplied with nutriment by the direct transmission of organizable materials from the circulating fluid of the mother to its own; but obtains it by the processes of digestion, absorption, and assimilation, which involve the establishment of new modes of vital activity in its own organism. In order, however, that the change may not be too sudden, the nutriment provided by Nature for the early period of infantile lise, is such as to occasion the least possible demand upon its vital powers, for the preparation of the organizable material which is required for its further growth and development. But the transition is a most important one in another particular; the infant is now thrown in a great degree upon its own

resources for the generation of its Heat; the necessary combustion being promoted by the arrangements for that active Respiration, which now supersedes the very limited aëration of its circulating fluids that was sufficient during fœtal life. In the movements of the respiratory muscles and of the walls of the alimentary canal, we have a new source of expenditure of vital force, and of destruction of tissue; and this expenditure is progressively augmented, as the motions of the body and limbs become increasingly active. Thus we find that the formative powers are not exercised during Infancy and Childhood, solely in the *construction* and *augmentation* of the fabric (as they were during embryonic life), since there is a constant demand upon them for its *maintenance;* and this demand becomes greater, and greater, in proportion to the activity of the Animal powers. These, at first called into exercise by the stimulus of sensory impressions upon the Nervous system, are speedily brought into very energetic operation. This operation is of an extremely limited character, being at first purely *sensorial*, and for some time afterwards simply *perceptive*. But the *whole Mind* (such as it is) being given up to it, *habits of observation* are formed, which are never subsequently lost; the infant learns *how to use* his Organs of Sense; and he also acquires those powers of *interpreting* their indications, which become so completely engrafted into his nature, as henceforth to seem a part of it. Although this Education of the Senses will necessarily go on, even without any intentional assistance on the part of others, yet it is in the power of the Mother or Nurse to promote it effectually, by supplying objects of various kinds which the Infant may look at and grasp, and by not abruptly interfering (by the too speedy withdrawal of such objects) with the process by which the visual and tactile perceptions are blended and harmonized (§ 576).—The Nervous system of the Infant, although thus called into extraordinarily energetic activity, cannot long sustain that activity; a very large measure of Sleep is required for the restoration of its speedily exhausted powers; and any unsual excitement of them tends to injurious disturbances of its nutrition. It is owing to this peculiar susceptibility of the Nervous system of the infant to external influences, that medicines (especially narcotics) which exert a special influence upon that system, are so peculiarly potent in their effects at this period of life, that the greatest caution is needed in their administration.

824. The most important developmental change which occurs in Infancy, after the complete establishment of the extra uterine circulation (§ 741), is the completion and eruption of the first set of Teeth; the greater part of whose formation, however, has taken place before birth. These 'milk' or 'deciduous' teeth, 20 in number, usually make their appearance in the following order;—The four central Incisors first present themselves, usually about the 7th month after birth, but frequently much earlier or later; those of the lower jaw appear first. The lateral Incisors next show themselves, those of the lower jaw coming through before those of the upper; they usually make their appearance between the 7th and 10th months. After a short interval, the anterior Molars present themselves, generally soon after the termination of the 12th month; and these are followed by the Canines, which usually protrude themselves between the 14th and 20th months. The posterior Molars are the last, and the most uncertain in regard to their time of appearance; this varying from the 18th to the 36th month. In regard to all except the front teeth, there is no settled rule as to the priority of appearance of those in the upper or under jaw; sometimes one precedes, and sometimes the other; but in general it may be stated that whenever one makes its appearance, the other cannot be far off. The same holds good in regard to the two sides, in which develop-

ment does not always proceed exactly *pari passu*.—The period of Dentition is sometimes one of considerable risk to the Infant's life; and this especially when an irritable state of the nervous system has been brought about by unsuitable food, unwholesome air, or some other cause of disordered health. In such cases the pressure upon the nerves of the gum, which necessarily precedes the opening of the sac and the eruption of the tooth, is a fruitful source of irritation; producing disturbance of the whole system, and giving origin to Convulsive affections which are not unfrequently fatal. These have been particularly studied by Dr. M. Hall, who recommends the free use of the gum lancet, as a most important means of prevention and cure; but the Author has no doubt that too much attention has been given to the immediate source of the irritation, and too little to the general state of the system; and that constitutional treatment, especially change of air, and improvement of the diet, is of fundamental importance. In infants whose general health is good, and who are not over-fed, Dentition is usually a source of but very trifling disturbance; a slight febrile action, lasting only for a day or two, being all that marks the passage of the tooth through the capsule; and its eruption through the gum taking place without the least indication of suffering or disorder. Any existing malady or abnormal tendency, however, is pretty sure to be aggravated during the 'cutting of the teeth;' and it is therefore of the greatest consequence, that the infant should be withdrawn during this period from all injurious influences; and that no irregularity of diet, or deficiency of fresh air and exercise, should operate to its disadvantage.

825. Although there are no well-marked divisions between the periods of Childhood, Youth, and Adolescence, through all of which we witness the continuance of the processes of Growth and Development (though in a gradually decreasing ratio), yet we may appropriately distinguish each as the epoch of one of those important changes which tend towards the completion of the fabric—namely, *Childhood* as ranging through the greater part of the period of the second Dentition—*Youth* as characterized by that increased evolution of the sexual organs, and by those general constitutional changes accompanying that evolution, which altogether constitute Puberty,—and *Adolescence* as distinguished by that entire consolidation of the Osseous skeleton, which is not completed until the full stature has been attained. It will be convenient first to consider what is common to all these periods; and then to notice the features by which they are severally characterized.

826. The passage from Infancy to Childhood may be regarded as marked by the eruption of the 'deciduous' Teeth; by the termination of that direct supply of food to the offspring, which is afforded until then by the mammary secretion of the mother; by the dawn of the Intellectual powers, manifested in the first efforts at speaking; and by the acquirement of sufficient control over the muscular apparatus, to render it subservient to the increasing desire which then displays itself for independent Locomotion. All these advances usually take place simultaneously, or nearly so, during some part of the second year; some Infants being much more forward than others, both in 'cutting their teeth' and in learning to walk and to talk. When they have been completed, the Child enters upon a life which is in many respects new. The alteration of its diet involves a much higher activity of all the organs which are concerned in making blood; whilst its greatly increased amount of exertion, both of body and mind, gives occasion to a more rapid disintegration of the nervous and muscular tissues, and hence to a higher activity of the Excretory organs. This will, of course, progressively augment, in proportion as the Nervo-muscular apparatus is brought, with advancing years, into more

vigorous and more prolonged exercise; until, with the attainment of adult age, the disintegration of these tissues comes to be the chief source of the Excrementitious products. But during the whole period of increase there is another source of demand for nutritive activity, in that perpetual *reconstruction* of the fabric (involving a sort of continual pulling down and rebuilding on a larger scale, all the old materials being carried away as useless) which is a necessary condition of its growth: but this demand of course slackens with the diminution of the rate of increase; and at last it ceases altogether, just when the other attains its maximum. Hence the demand for food, on the one hand, and the amount of excretory matter set free from the body, on the other, are remarkably large during the whole of this period; the child, as every one knows, consuming far more nutriment than the adult, in proportion to the weight of their respective bodies; and the like being true of the quantity of carbonic acid exhaled from the lungs and of the urea given off from the kidneys.—That the germinal capacity, though inferior to that of the embryo, still persists in a high degree during the period of childhood and youth, is shown in the readiness with which the effects of injuries and disease are recovered from; for although the regeneration of lost parts does not take place to nearly the same extent as during early embryonic life, yet up to a certain point it is effected with great completeness, and with much greater rapidity than at later epochs. It is still, in fact, rather in the exercise of formative power, than in the production of nervo-muscular vigour, that the vital force of the earlier part of this period is displayed; and we may readily trace such a relation of reciprocity between these two modes of its manifestation as is strongly indicative of the community of their source. For it is familiar to every observer, that, when the growth of a child or a young person is peculiarly quick, his nervo-muscular energy is usually feeble, and his power of endurance brief, in comparison with that which can be put forth by one whose frame is undergoing less rapid increase. And we observe, moreover, that the capacity of resistance to depressing influences of various kinds, which is a no less decided manifestation of the vital power of the organism (seeing that these influences are of such a kind as to *tend towards* its death), is possessed by the latter in a far higher degree than by the former. This is remarkably the case in regard to privation of food and depression of external temperature; under which, too, children and young persons succumb much more speedily than adults.

827. It is most interesting to trace, during the progress of the development of the bodily fabric, the gradual expansion and invigoration of the Mental powers. The acquirement of Language constitutes the most important step in the development of the *ideational* consciousness; and it is easy to recognize in the psychical manifestations of Children, the further progress of that development. The formation of *Associations* between ideas takes place with extraordinary readiness and tenacity during the earliest period of childhood; and these exercise so much influence over the succession of the thoughts during the whole remainder of life, that "the force of early associations" has become proverbial. Out of these associations arise, on the one hand, Memory and Imagination; on the other hand, those simple processes of Reasoning which are necessary to the development of a higher class of ideas. Thus the mind passes from those primary notions of individual objects which are directly suggested by sense perceptions, to those *abstract* ideas of their qualities, which enable them to recognize those qualities elsewhere, notwithstanding the existence of differences in other respects; and thence to those *general* ideas, in which the abstractions are embodied. In all these processes, the child mind

seems to be so entirely concentrated upon the particular subject of its thoughts, as to be 'possessed' by it for the time, almost as completely as a 'hypnotised' subject is by his dominant idea; and no prolonged study of it is required to justify the statement, that its operations are for some time entirely *automatic*, and that the acquirement of Volitional control over them, on the part of the individual, is a very gradual process. As a general rule it may be laid down that the activity with which the formation of new ideas takes place in the child and the rapidity with which the attention transfers itself from one object to another, prevents any single state from fixing itself durably in the consciousness, so that the Memory preserves but faint traces of the greater part of what passes through the mind; and it is (for the most part) only when the same thoughts are frequently recurred to, that they take root (so to speak) in the psychical nature. Still we occasionally find that particular impressions exert a very powerful influence on the subsequent course of thought and feeling; and there is good reason to believe that even where the *consciousness* loses its hold over them, impressions of a transient nature may leave such traces in the Brain, that they may be reproduced at any future time when the appropriate suggestion may happen to be supplied.—Whilst the ideational consciousness is thus being expanded and elevated, the *Emotional* part of the Psychical nature is rapidly acquiring a greater range and intensity of action. The infant and young child give ample evidence in their actions of the several forms of Emotional Sensibility which connect themselves with Sensational and Perceptive states; but no sooner does the development of Ideas commence, than the various modifications of 'feeling' attach themselves to *these;* and thus almost every thought that is not a purely intellectual abstraction, comes to possess more or less of an Emotional character. Here, again, we trace the powerful influence of early impressions; for notwithstanding that the state of feeling which is habitual to each individual may depend in great degree upon his original constitution, yet it is unquestionable that it is largely influenced (especially in its association with particular classes of ideas) by *sympathy* with the like states in those among whom the child receives its early education. It is of peculiar importance, therefore, that this example should be such as it is wholesome for the child to imitate; since it is upon the habits of feeling thus early formed, that the happiness and right conduct of after life mainly depend. This statement (which applies with yet greater force to the Moral Sense) may at first seem inconsistent with the well-known fact that the Emotions of children are peculiarly transient in their character, even when they are violently excited; one state of feeling giving place to another, even of the most opposite kind, under the influence of some new impression or of some change in the direction of the ideas. But the same general principle applies to this case, as to the formation of habits of thought—namely, that although individual impressions are more speedily dissipated from the minds of children than from those of adults, yet that when impressions of the same kind are frequently repeated, the brain *grows to* them in such a manner that they come to take part (as it were) in its ordinary working; and thus, by establishing a particular mode of nutritive assimilation, they tend to *perpetuate* this acquired habit, of whatever nature it may be.—The right training of the Emotional tendencies and all the higher uses of the Intellectual Faculties, depend in great degree, as may readily be shown, upon the influence of the Will in directing the current of thought and feeling; and this becomes greater and greater, if rightly cultivated, with the advance of years, so that the psychical powers, whilst themselves acquiring an increase of vigour and comprehensiveness, are brought more and more under the control of the individual, and can be utilized in any

way in which he may choose to employ them. Thus, with a diminishing *mobility* of thought and *excitability* of feeling, the Mind becomes more and more capable of *sustained* and *determinately-concentrated* activity; and is at the same time progressively acquiring that store of familiar *experiences*, which not only constitutes the basis of all attainments in special departments of knowledge, but supplies (when judiciously used) that 'common sense' by which we form most of our judgments and direct most of our conduct.—During this period, moreover, the Muscular apparatus of animal life, whose actions are at first purely automatic, is brought more and more under the direction of the Mind, so as to express its ideas, its feelings, and its volitions. And it is whilst this transference is going on, that new habits of action are most readily formed, and when once formed, are durably impressed upon the organism.—The excess which must exist, during the whole of this period, in the *constructive* over the *destructive* activity, and the large amount of the latter which (as already shown) arises out of the very nature of Growth, in addition to that which proceeds from the increased activity of the Animal functions, necessitates a much larger proportion of repose than suffices for the adult; but this necessity diminishes with the progress of years, for the reasons already mentioned; and thus we find that whilst the young child passes 16 or 18 hours a day in sleep, half that time suffices for the youth just entering on manhood.

828. The *Second Dentition*, consisting in the replacement of the *deciduous* or 'milk' Teeth by the *permanent* Teeth that succeed them, which is the most important developmental change that occurs during the period of Childhood, normally commences in the 7th or 8th year: the germs of the new teeth, however, are formed long previously, having their origin in a process of gemmation from the tooth-sacs of the temporary teeth, which takes place at a very early period in the development of the latter.* The three permanent Molars on either side of each jaw, however, have no such origin; since they do not replace temporary teeth. The first pair, which usually make their appearance behind the temporary molars, either contemporaneously-with, or a little anteriorly-to, the first shedding of the deciduous teeth, are really 'milk' teeth, so far as their origin is concerned, since they are developed from primitive tooth-sacs: on the other hand the second true molars, which afterwards come up behind them, are evolved from tooth-sacs, which hold the same relation to those of the first, as the tooth-sacs of the other permanent teeth do to those of the deciduous teeth which they replace; and the third true molars, or *dentes sapientiæ*, bear the like relation to the second. Although the eruption of the true molars is so long postponed, yet the foundation of them is laid at an earlier period; for the papilla of the *first* is distinguishable at the 16th week after conception, that of the second at the 7th month after birth, and that of the third at the 6th year. In the successive replacement of the 'milk' teeth by the 'permanent' set, a very regular order is usually followed. The middle Incisors are first shed and renewed, and then the lateral Incisors. The anterior 'milk' Molars next follow; and these are replaced by the anterior Bicuspid teeth. About a year afterwards the posterior 'milk' Molars are shed, and are replaced in like manner by Bicuspid teeth. The Canines are the last of the 'milk' teeth to be exchanged; in the succeeding year, the second pair of the true Molars appear; but the third pair, or *dentes sapientiæ*, are seldom developed until three or four years subsequently, and often much later.

829. It has been proposed† (and from the evidence adduced in its favour

* See Mr. Tomes' "Manual of Dental Anatomy."

† "The Teeth, a Test of Age, considered with reference to the Factory Children." By Edwin Saunders.

the proposition would seem entitled to considerable attention) to adopt the successive stages in the Second Dentition as standards for estimating the physical capabilities of Children, especially in regard to those two periods which the Factory-Laws render it of the greatest importance to determine—namely, the ages of *nine* and *thirteen* years. Previously to the former, a Child is not permitted to work at all; and up to the latter, it may be only employed during nine hours a day. The necessities or the cupidity of Parents are continually inducing them to misrepresent the ages of their children; and it has been found desirable, therefore, to seek for some test by which the capability of the Child may be determined, without a knowledge of its age. A standard of height has been adopted by the Legislature for this purpose; but upon grounds which, physiologically considered, are very erroneous; since, as is well known, the tallest children are frequently the weakliest. According to Mr. Saunders, the degree of advance of the Second Dentition may be regarded as a much more correct standard of the degree of general development of the organic frame and of its physical powers; and it appears from his inquiries that it may be relied on as a guide to the real age in a large proportion of cases; whilst no serious or injurious mistake can ever arise from its use. It may happen that local or constitutional causes may have slightly retarded the development of the Teeth; in which case the age of the individual would rather be under-estimated, and no harm could ensue: on the other hand, instances of premature development of the Teeth very rarely, if ever, occur; so that there is little danger of imputing to a Child a capability for exertion which he does not possess, as the test of height is continually doing. Moreover, if such an advance in Dentition should occur, it might probably be regarded as indicative of a corresponding advance in the development of the whole organism; so that the real capability would be such as the teeth represent it.—The following is Mr. Saunders's statement of the Ages at which the 'permanent' Teeth respectively appear:—The first true Molars usually present themselves towards the end of the 7th year. Occasionally one of them protrudes from the gum at 6, or more frequently at 6½ years of age; but the evolution of the whole of them may be regarded as an almost infallible sign of the Child being 7 years old. In other instances, where the tooth on one side of the mouth is freely developed, it is fair to reckon the two as having emerged from their capsules; since the development of the other must be considered as retarded. This rule only holds good, however, in regard to teeth in the same row; for the development of the teeth in either jaw must not be inferred from that of the coresponding teeth in the other. With this understanding, the following Table will probably be very near the truth:—

Central Incisors developed at	8 years.
Lateral Incisors	9 „
First Bicuspid	10 „
Second Bicuspid	11 „
Canines	12 to 12½
Second Molars	12½ to 14

The following are the results of the application of this test, in a large number of cases examined by Mr. Saunders. Of 708 children of *nine* years old, 530 would have been pronounced by it to be near the completion of their *ninth* year; having the central, and either three or four lateral, incisors fully developed. Out of the remaining 178, it would have indicated that 126 were 8½ years old, as they presented one or two of the lateral Incisors; and the 52 others would have been pronounced 8 years old, all having three or four

of the central Incisors. So that the extreme deviation is only 12 months; and this in the inconsiderable proportion (when compared with the results obtained by other means) of 52 in 708, or 7⅓ per cent. Again, out of 338 children of 13 years of age, 294 might have been pronounced with confidence to be of that age; having the Canines, Bicuspid, and second Molars, either entirely developed, or with only the deficiency of one or two of either class. Of the 44 others, 36 would have been considered as in their 13th year, having one of the posterior Molars developed; and 8 as near the completion of the 12th, having two of the Canines, and one or two of the second Bicuspid. In all these instances the error is on the favourable side—that is, on the side on which it is calculated to prevent injury to the objects of the inquiry; in no instance did this test cause a Child to be estimated as older or more fit for labour than it really was.*

830. The period of *Youth* is distinguished by that advance in the evolution of the Generative apparatus in both sexes, and by that acquirement of its power of functional activity, which constitutes the state of *Puberty*. Of the principal changes in which this consists, in the two sexes respectively, an account has already been given (§§ 693, 699); and it is merely requisite here to add, that this augmented development can only be rightly regarded as *preparatory* to the exercise of these organs, and not as showing that the aptitude for their exercise has already been fully attained. It is only when the growth and development of the *individual* are completed, that the procreative power can be properly exerted for the continuance of the *race;* and all experience shows that by prematurely and unrestrainedly yielding to the sexual instincts, not merely the generative power is early exhausted, but the vital powers of the organism generally are reduced and permanently enfeebled; so that any latent predisposition to disease is extremely liable to manifest itself; or the bodily vigour, if for a time retained with little deterioration, early undergoes a marked diminution.

831. After the attainment of Puberty, no marked alteration takes place in the organism, save the continuance of its increase in stature, usually for a few years longer; which increase is the chief manifestation of the excess of the germinal capacity, that has not yet expended itself in the building up of the fabric. But so long as this increase is going on there is a want of that solidity and compactness of the organism which seem only attainable when growth has ceased; and the attainment of which, being essential to the highest manifestations of vigour and endurance, marks the final completion of its development. Of this we have the best illustration in the *Osseous* system; whose completion, being postponed until all further *growth* has ceased, may be fairly considered as marking the final stage in the development of the organism, and as therefore characterizing the period of *Adolescence*.—Commencing with the *Vertebral Column*, we find that whilst the 'body' and 'neural

* The value of this test, as compared with that of Height, is manifested by a striking example adduced by Mr. Saunders. The height of one lad, J. J., aged 8 years and 4 months, was 4 feet and ¾ of an inch; that of another boy, aged 8 years and 7 months, was only 3 feet 7¼ inches. According to the standard of height adopted by the Factory Commissioners (namely, 3 feet 10 inches), the *taller* lad would have been judged fit for labour, whilst the *shorter* would have been rejected. The Dentition of the latter, however, was further advanced than that of the former; for he had two of the lateral Incisors, whilst the former had only the central: and the determination of their physical powers, which would have been thus formed, would have been in complete accordance with the truth. The elder boy, though shorter than the other by 5½ inches, possessed a much greater degree both of corporeal and mental energy, and his pulse was strong and regular; whilst that of the younger lad, who was evidently growing too fast, was small and frequent.—An instance even more striking has come under the Author's own observation.

arches' of each vertebra become consolidated in early childhood, the spinous and transverse processes are completed by separate 'epiphyses,' the ossification of which does not commence until after puberty, and the final union of which with the body of the bone may not occur until the age of twenty-five or thirty years. About the same time, there is formed and added to each surface of the body of the vertebra a smooth annular plate of solid bone, which covers a portion that was previously rough and fissured. During this period, the consolidation of the Sacrum is proceeding; the component vertebræ of which remain separate up to about the sixteenth year, and then begin to unite from below upwards, the union of the two highest being completed by about the twenty-fifth or the thirtieth year; whilst at the same time thin osseous plates are formed on either side of the coalesced mass, which seem to represent the epiphyses of the transverse processes of its component vertebræ, and like them are finally joined on to the body of the bone. The ossification and coalescence of the Coccygeal vertebræ takes place at a still later period. Each Rib in like manner has two epiphyses, one for the head and the other for the tubercle; the ossification of which begins soon after puberty, whilst their union with the body of the bone is not completed until some years afterwards. The five pieces of which the sternum consists, though themselves completely ossified, remain separate until after the age of puberty; when their union commences from below upwards, as in the sacrum, not being always completed, however, even in old age, by the junction of the first piece to the rest of the bone. The ossification of the Ensiform cartilage does not commonly begin until after the age of puberty; and it is usually not entirely completed even in very advanced life. The ossific union of the separate elements of the *Bones of the Skull* (§§ 751, 752), is usually completed within a few years after birth: but there are some parts which not unfrequently remain distinct during the greater portion of life, and which may even never coalesce; such is the case with the two halves of the Frontal bone, which often remain permanently divided by a continuation of the sagittal suture, and with the Styloid process of the temporal bone. In the *Upper extremities* we find the Scapula presenting three epiphyses, one for the coracoid process, one for the acromion, and one for the lower angle of the bone; the ossification of which begins soon after puberty, their union with the body of the bone taking place between the ages of twenty-two and twenty-five years. The Clavicle has an epiphysis at its sternal end, which begins to form between the eighteenth and twentieth years, and is united to the rest of the bone a few years later. The consolidation of the Humerus is completed rather earlier; the large piece at the upper end, which is formed by the coalescence of the ossific centres of the head and two tuberosities, unites with the shaft at about the twentieth year; whilst its lower extremity is completed by the junction of the external condyle and of the two parts of the articulating surface (previously united with each other), at about the seventeenth year, and by that of the internal condyle in the year following. The superior epiphyses of the Radius and Ulna unite with their respective shafts at about the age of puberty; the inferior, which are of larger size, at about the twentieth year. The epiphyses of the Metacarpal and Phalangeal bones are united to their principals at about the twentieth year. In the *Lower extremities* the process of ossification is completed at nearly the same periods as that of the corresponding parts of the upper. The consolidation of the Ilium, Ischium, and Pubis, to form the Os Innominatum, by the ossification of the triradiate cartilage that intervenes between them in the acetabulum, does not take place until after the period of puberty; and at this time additional epiphyses begin to make their appearance on the crest of the ilium, on

its anterior inferior spine, on the tuberosity of the ischium, and on the inner margin of the pubes, which are not finally joined to the bone until about the twenty-fifth year.

832. The rapid increase in *Viability* which shows itself in both sexes up to the age of puberty, its rapid decline from that point, and its subsequent increase in the male up to the age of thirty, have been already pointed out (§ 761). The disorders to which the organism is most subject during the several periods which have now been considered, are by no means the same for each. In early Childhood, when there is a great demand for the activity of the Digestive and Assimilative functions, and these have to be exercised upon nutriment to which their organs are not yet accustomed, we find derangements of those organs to be among the most common of all maladies; these may be serious enough in themselves to constitute dangerous and even rapidly fatal diseases; but even when they do not take these acute forms, a foundation is often laid, in habits of perverted Nutrition thence arising, for disorders of a more chronic nature (especially those depending on the Tubercular diathesis), which may not manifest themselves for many years afterwards. The peculiar activity of the nervous centres, which is prolonged from Infancy into early Childhood, involves a continued liability to derangements of *their* nutrition or of their functions; and thus it happens that in young children of scrofulous temperament, it is either in the mesenteric glands, or in the brain or its membranes, that tubercular deposit first takes place. The second Dentition, like the first, is often accompanied with a great deal of constitutional disturbance; especially in such individuals as are suffering from defective Nutrition, or from an irritable state of the Nervous System. In the former case there is a special proneness to Tubercular disease;* in the latter, to Epilepsy, Chorea, or some other form of disorder of the nervous centres, the connection of which with Dentition is shown by its abatement when that epoch has passed. A large part of the sickness and mortality, however, which presents so high a rate during the whole period of Childhood, is due to various forms of Zymotic disease, especially the Exanthemata and Infantile Remittent Fever, and to their *sequelæ*.†—The attainment of Puberty in the Male sex is not usually attended with any specific tendency to disease; nor would it probably be in the Female, if her mode of life were more accordant with the rules of health. Although disorder of the Menstrual function is one of the most common phenomena of female youth, yet it is undoubtedly to be looked upon more frequently as a symptom of general defect of nutrition (and especially of an impoverished condition of the blood), than as itself constituting a disease. The extraordinary reduction in the probability of life, indicating a large mortality, during the years which immediately succeed puberty, seems to depend in great degree, in the Male, upon the premature use of his generative powers, and upon his entrance upon the active employments of life before his constitution has received that invigoration which results from the completion of his bodily development; whilst in the female it is very commonly attributable to the accumulation of unhealthy influences, which begin to 'tell' upon the powers of her system, when its germinal capacity no longer

* It is a very significant circumstance, that of the many specimens of the Anthropoid Apes which have been brought alive into this country, not one has survived its second dentition; and that, in almost every case, it has been by tubercular disease that their lives have been thus prematurely cut-off.

† The effects of affluence and poverty on the duration of life at this period are remarkably shown by the deductions of Caspar of Berlin, who states as the result of his inquiries that 1000 children born in the families of affluent persons, 911 attained the age of 15 years; whilst of 1000 paupers, only 584 survived to that age. (Béclard, "Physiologie," 1862, p. 594.)

ministers to its active regeneration. It is *then*, in both sexes, though from causes whose immediate nature is different, that the Tubercular diathesis is prone to develop itself with peculiar intensity, and that, by fixing upon the Respiratory organs, it produces the most rapidly-fatal alterations in structures whose integrity is essential to life.

833. *Period of Maturity.*—The cessation of growth and the completion of the developmental process, which indicate the attainment of *Manhood*, are accompanied by a marked increase in the general vigour of the organism, and by a special augmentation in the power of *endurance* in the exercise of the Animal faculties. With the exception of those parts of the fabric whose utility was confined to the earlier periods of its development, we find every organ now presenting its greatest capacity for sustained activity; and thus it is from the characters which each presents at this period, that we base our ideas of its *typical* perfection of structure and composition. All the previous changes which the organism has undergone, both as a whole and in its separate parts, concur to the attainment of this perfection, as we have especially seen in regard to the evolution of the solid framework of the body; and every subsequent change, as we shall presently perceive (835), involves a deterioration from it. The whole *nisus* of development, during this period, appears to be directed towards the *maintenance* of the organism in the state which it had acquired at its commencement; by the regeneration of its tissues as fast as they undergo disintegration, and by the renovation of its vital force in proportion as this is expended. There is no longer any capacity for the production of new organs, and comparatively little for the augmentation of those already existing; the increase of the Uterine and Mammary structures, during the period of gestation, being the most important examples of formative power, and these presenting themselves in the sex in which there is least of nervo-muscular activity and of general vigour. We should infer then, that the 'germinal capacity' is now on the decline; and this further appears from the diminished energy and completeness with which the reparative processes are performed, as compared with the mode in which they are executed during the period of growth. There is consequently a less demand for alimentary material (allowance being made for the augmented bulk of the body) than during the previous periods; and the dependence of life upon a constant supply of aliment is far less close. Moreover, the ordinary rate of waste or degeneration of tissue is now much less rapid than during the period of growth; for we have seen that decay and removal, in the latter case, are among the very conditions of increase; whilst in the former, they proceed, for the most part, only from the expenditure of the vital powers of the tissues, consequent upon *their* functional activity. Hence it is upon the degree in which the *Animal* powers are exercised, that the demand for food chiefly depends in the Adult; the sole purpose of the Organic or Vegetative operations being (so to speak) to keep the apparatus of Animal life, now fully developed, in working order. The relative activity of the different parts of this apparatus is now somewhat modified. The *observing faculties* no longer possess the same pre-eminence; the *emotional sensibility* is less readily excited; but the *intellectual powers* now act, in the modes which have become habitual to them, with a sustained vigour and completeness which they never previously possessed. And so, whilst the muscles are not so easily excited to contraction, and new combinations of movement are acquired with far more difficulty than during the period of growth and development, the force which they can generate by their contraction is augmented, and this force can be kept-up for a much longer time in adults than in younger subjects.

834. The duration of the period over which this 'maintenance' may be protracted, without any sensible deterioration, depends in great degree upon the due observance of all the conditions of health. If the various mental and bodily faculties are duly exercised, without being overtasked—if an amount of sleep adequate to their periodic renovation be regularly taken—if a sufficient but not excessive quantity of wholesome food be ingested at appropriate intervals—if the functions by which the blood is prepared, and those by which it is kept in purity, be duly performed—if all such noxious agents as foul air, strong alcoholic liquors, and tobacco-smoke, be kept at a distance—and there be no constitutional predisposition to disease on the one hand, nor any exposure to extraneous morbific causes on the other—it may be fairly anticipated that the bodily and mental vigour may be sustained with little deterioration during a long succession of years. The circumstances that most tend to premature decline, are, on the one hand, excessive exertion either of the mental faculties or of the generative power; or, on the other, undue indulgence in food, or in stimulating drinks, or in any practice that tends to disorder the Organic functions, especially by exciting them to undue activity. Every one who, in *any* of these modes, may "live too fast," is almost certain to pay the penalty in an abbreviation of his term of vigorous activity; which may be either brought to a sudden and final close by fatal disease, or may be prematurely reduced by more gradual decay. And this tendency will of course be more decided, the greater is the amount, and the larger the combination, of those departures from the Laws of Health which give rise to it.

835. *Period of Decline.*—The *decline of life* exhibits a much more obvious diminution of the whole vital power of the organism; for not only is its formative activity now greatly reduced, but its nervo-muscular energy and general vigour progressively diminish, and its generative power becomes enfeebled, or ceases entirely (§§ 693, 701). Of this diminution in formative power we have evidence in the entire absence of any attempt at new development, in the less perfect and more tedious manner in which the losses of substance occasioned by disease or injury are recovered from, and in the gradual deterioration of the organism in general. The tissues which are rendered effete by their functional activity, are not any longer replaced in their normal completeness; for either the quantity of new tissue is inadequate, so that the bulk of the organs is obviously reduced; or their quality is rendered imperfect by the production of structures in various phases of degeneration, in place of those which had been previously developed in the fullest completeness. The inferiority of Nervo-muscular energy and of general vigour are thus evidently the result of the deficiency, and not (as in the period of growth) of the excess of formative power; and in proportion as the 'waste' of the tissues, consequent upon their functional activity, is more rapid than their renovation, a progressive loss of substance must take place. The forms of Degeneration most commonly met with in advanced age, are the *fatty* and the *calcareous*. The former is extremely prone to show itself in those organs whose integrity of structure is peculiarly important to health, and whose deterioration interferes directly with the *vital* properties of their component tissues. Thus we observe it in the Muscular apparatus generally, but pre-eminently in the walls of the Heart; and in proportion as its contractile fibre has been replaced by particles of fat, must the vital energy of any muscle be lowered. So, again, we find the same degeneration in the Liver, Kidney, and other parts of the Glandular apparatus; the proper secreting action of which is impaired in the ratio of the substitution of fat for

the proper Glandular elements. But it may also lead to most serious derangements of the vital functions, by its interference with the purely mechanical actions of certain parts of the organism; thus, fatty degeneration of the walls of the Blood-vessels is one of the most frequent causes of those extravasations of blood in the nervous centres, which give rise to the apoplexy and to the various forms of paralysis so common among the aged; and the same change occurring in the Bones, gives them that peculiar brittleness which they frequently exhibit in advanced periods of life. The general decline of the vital powers, which has received the name of 'climacteric disease,' appears traceable to the same source.*—The tendency of the calcareous degeneration (which especially affects the Cartilaginous and Fibrous tissues) is almost exclusively to interfere with the *mechanical* adaptations of the organism; producing an injurious rigidity in various structures which require a greater or less amount of flexibility for the normal performance of their functions. Thus it is very common for the cartilages of the ribs to become ossified in advanced life, so as to interfere with the free movement of the walls of the thorax; and the thyroid cartilages of old people are frequently converted into bone, producing a roughness of the voice, and deficiency of the power of modulating it. The intervertebral substance (which is partly cartilaginous and partly fibrous) not unfrequently becomes solidified in the lumbar region, as do also the spinal ligaments, so that several of the lower vertebræ are firmly anchylosed to each other and to the sacrum; and a like change often takes place in the pelvic articulations, so that the pelvis and the lower part of the spine become one continuous mass of bone, destitute of flexibility or yieldingness in any part. In like manner the cranial sutures often become obliterated, and calcareous deposits occur in the duplicatures of the dura mater forming the falx and tentorium. A large amount of this kind of change may take place without any serious interference with the organic functions, although it tends to curtail the Animal powers. When the calcareous degeneration, however, extends itself to the vital organs, the interruption which it occasions in their actions may be fatal; thus, next to fatty degeneration, there is probably no more frequent cause of failure of the heart's action, or of extravasation from the blood-vessels, in old persons, than ossification of the valvular apparatus of the former, depriving it of the flexibility which is essential to its proper action, or the fibrous walls of the latter, imparting to them a brittleness which predisposes to rupture.†

836. Thus, then, with the advance of Old Age, the organism becomes progressively more and more unfit for the active performance of its vital operations; a gradual weakening is observable in the Mental as well as in the Corporeal energy; and a retardation becomes obvious in the current of Organic life. The mind is far less active than in the periods of Maturity; the perceptions are dull, the feelings comparatively obtuse (save where some dominant emotion has gained possession, through the previous habit of yielding to it), the intellectual powers cannot be so readily put in action, and the imagination loses its vividness. There are few instances in which any great works, either literary or artistic, have been executed after the age of threescore. Still the experience of a long life gives value to the judgment; and the counsels of the old, where the bearings of the question can be fully

* See Gulliver in the "Transact. of Roy. Med.-Chir. Soc.," 1843; and in "Edin. Med. and Surg. Journ.," 1843; Mr. Barlow's 'General Observations on Fatty Degeneration,' in the "Medical Times and Gazette," May 15, 1852.

† A good account of these changes will be found in the "Practical Treatise on the Diseases and Infirmities of Advanced Life," by Daniel Maclachan, M.D., 1863.

understood, deserve the respect of the young, more especially in cases where temporary ardour of feeling tends in the latter to supersede the dictates of their calmer reason.—The mental torpor is correlated, there seems no reason to doubt, with changes in the condition of the Nervous substance, which impair its original activity; and like changes, occurring in the Muscular substance, diminish its capacity for physical exertion. Hence there is, on the one hand, a marked diminution in the demand for food; on the other, a like diminution in the rate of the excretory processes, as is seen especially in the exhalation of carbonic acid (§ 287) and in the excretion of Urea: and in accordance with all these reductions, there is a greatly diminished power of sustaining the heat of the body, the temperature of which consequently becomes liable to a serious depression from external cold. This retardation of vital activity gradually becomes more and more marked, until, if neither accident nor disease should intervene, the current stops of itself; the formative power seems to undergo a progressive exhaustion, until no assistance from artificial heat, no supply of the most nutritious food, can any longer avail for the generation of new tissue; the nervo-muscular energy gradually declines, until at last even those actions on which the circulation and respiration entirely depend can no longer be performed; and with the cessation of these functions, the Life of the entire organism becomes extinct. —Such we may consider to be the mode in which *Death* normally occurs. Various abnormal influences, however, remain to be considered, which may bring about this final result at an earlier period, and in different modes (CHAP. XXI.).

CHAPTER XXI.

OF DEATH.

837. We have seen it to be inherent in the very nature of Vital Action, that it can only be sustained during a *limited period* by any Organized body; for although the duration of certain structures may be prolonged, and their vital properties retained, almost indefinitely, yet this is only when the withdrawal of all extraneous agencies has reduced them to a condition of complete inactivity. The Organized fabric, in fact, is at the same time the *instrument* whereby Vital Force is exercised, and the *subject* of its operation; and of this operation, *decline* is no less a constituent part than *development*, and *Death* is its necessary sequence. Hence, in the performance of each one of those Functions whose aggregate makes up the Life of Man, the particular organ which ministers to that function undergoes a certain loss by the decline and death of its component tissues; and this the more rapidly in proportion to the activity of the changes which are effected by their instrumentality. But if the regenerative processes be also performed with due vigour, no deterioration of the organ is manifested, since every loss of substance is compensated by the production of an equivalent amount of new and similar tissue. This regenerative power, however, gradually diminishes with the advance of years; and thus it happens that the entire organism progressively deteriorates (§ 835), and that Death at last supervenes from a general failure of the vital powers, rather than from the perversion or cessation of any one class of actions in particular.

838. But Death may occur at any period of Life, from some local interruption produced by disease or injury in the regular sequence of vital actions; such interruption extending itself from the part in which it commences to the

organism in general, in virtue of that intimate mutual dependence of one function upon another, which is characteristic of all the higher orders of living beings. The death of the body as a whole, which may be appropriately designated *Somatic** death, becomes a necessary consequence of the death of a certain part of it, or *Molecular* death, only when the cessation of activity in the latter interferes with the elaboration, the circulation, or the depuration of the Blood, which supplies not merely the nutritive *pabulum* to every part of the organism, but also the oxygen which is essential to the activity of the Nervo-muscular apparatus. Thus, even in the higher animals, the death or removal of the limbs, although they may constitute (as in Man) a large proportion of the fabric, is not necessarily fatal; because it involves no interruption, either in the nutritive operations of the viscera, or in the sensorial functions of the brain.† On the other hand, the destruction of a certain minute portion of the Nervous centres, or such a lesion of the Heart's structure as would be trivial in almost any other organ, may be the occasion of immediate death; because these changes arrest the Respiratory movements, or interfere directly with the action of the Heart, so as to bring the flow of blood to a stand. It sometimes happens, however, that life may be prolonged after the death or removal of some important organ, in consequence of the power which some other possesses of discharging its functions; thus we find that in Man the kidneys seem occasionally to take upon themselves the elimination of the constituents of bile from the blood (§ 368); and in the Frog the skin can perform part of the office of the lungs, so as to effect the aëration of the blood in a sufficient degree to prolong life for some time, unless the temperature be elevated.‡

839. But although the vital activity of every part of the body is dependent upon a due supply of circulating fluid, yet this dependence is usually not so close as to involve the *immediate* suspension of vital activity, or *Molecular Death*, in every part, whenever the general Circulation shall have been brought to a stand. For we have have distinct evidence of the persistence of vital changes in various organs and tissues of the body, after the death of the body at large; as is manifested in the performance of ciliary and of muscular movements, in acts of secretion and perhaps even of nutrition,§ in the maintenance of the local circulation, and in the generation of animal heat (§ 384); and the fact is even yet more remarkably manifested in the reunion (even after the lapse of some hours) of parts that have been entirely severed, such as

* This term was first suggested by Dr. Prichard, in place of the less accurate term 'systemic' which was previously in use. (See "Cyclop. of Anat. and Physiol.," vol. i. p. 791.)

† The Author has been informed by Dr. Daniell that it is not at all uncommon in Negroes who are in the last stage of the adynamic fevers of the African coast, for death and decomposition to extend gradually upwards from the extremities to the trunk; so that the former may be in a state of absolute putrescence, before the respiration and circulation have been brought to a stand: and he learns from Prof. Jackson, of Philadelphia, that he has more than once witnessed the same occurrence.

‡ That such cannot take place in Man, is due not merely to the far less complete adaptation of his skin for the aëration of the blood, but also to the difference in the type of his circulation, which causes the arrest of blood in the pulmonary vessels to produce a stagnation of the entire current.

§ Thus Mr. T. Bell mentions ("History of British Reptiles," p. 61), that having been engaged in the careful dissection of the poison-apparatus of a large Rattlesnake, although the animal had been dead for some hours, and the head had been taken off immediately after death, yet the poison continued to be secreted as the dissection proceeded, so as to require to be occasionally dried off with a bit of sponge.—A growth of Hair is said to have been noticed in several instances after death; and if the temperature of the surrounding medium be not too low for the vital activity of the hair-bulbs, there seems no adequate reason why this should not take place.

fingers or toes, noses or ears, by adhesion between the cut surfaces when brought into apposition, which could not take place if the severed part were already *dead*.

840. The permanent and complete cessation of the Circulating current, which essentially constitutes *Somatic* Death, may be directly or indirectly consequent upon several distinct causes. In the *first* place, it may be due to failure in the propulsive power of the Heart, which constitutes *Syncope*. This failure may occur either (*a*) in consequence of a loss of the proper irritability of the Muscular tissue, or (*b*) through the supervention of a 'tonic spasm,' the organ remaining rigidly contracted without its usual alternation of relaxation. The phenomena attending death in the two cases are not dissimilar, when the loss of irritability is sudden and immediate (as when it arises from violent impressions on the nervous system); for the individual suddenly turns pale, falls back or drops down, and expires with one gasp. But under the former condition, the heart is found *flabby*, sometimes empty, sometimes distended with blood, both cavities being equally filled; whilst in the latter the heart is contracted and hard, containing little or no blood, as when in the state of *rigor mortis*.—The cause of the loss of irritability, when sudden, usually lies in the influence of a 'shock' transmitted through the Nervous system, and originating either in some severe lesion of its central organs or of its peripheral expansion (§ 227), or in a deficiency of its supply of blood or diminution of its usual pressure (such as is produced by rapid detraction of blood, especially in the erect posture, by the rapid removal of the fluid in ascites without the substitution of artificial pressure, or by suddenly rising into the erect posture, after prolonged recumbency,* still more, after long stooping), or in some powerful mental emotion, either exciting or depressing. A more gradual effect of the same kind is produced by severe lesions of the internal organs (such as rupture of the uterus), which often prove fatal by the general 'collapse' thus induced, rather than by the disturbance which takes place in their own proper functions; and this seems to be the usual *modus operandi* of corrosive poisons, whose effect upon the heart's action resembles that produced by severe burns of the surface in children. The influence of the proper *sedative* poisons, however—such as digitalis, tobacco, aconite, and upas—seems to be directly exerted, through the blood, upon the tissue of the heart itself; and the same is probably the case with some of those 'morbid poisons,' whose introduction into the system gives rise to diseases of the most intensely adynamic type, such as Malignant Cholera, in which the 'collapse' is out of all proportion to any local lesion. But, again, the loss of the Heart's irritability may be a gradual process, resulting from the deterioration of its tissue by fatty degeneration or by simple atrophy; and this last condition may be due to deficiency of blood, as happens in chronic starvation and diseases of exhaustion, in which the failure of the circulation seems due to the weakening of the heart's power and to the lowering of the quantity and quality of the blood, acting as concurrent causes, the condition thus induced being appropriately designated *Asthenia*. In all cases it is to be observed that when the Vital powers have been previously depressed, a much slighter impression on the Nervous system is adequate to produce Syncope, than would be required when it is in a state of full vigour.—The causes of the tonic spasm of the heart have not been clearly made out; but it seems producible, like the

* Hence it is that great caution should be exercised in allowing patients who are convalescent from acute diseases to rise into the erect position, many cases of fatal syncope having been thus induced. The state of general debility, and the continued recumbency both favour this result, especially in persons advanced in life.

more common form of Syncope, by agencies operating through the Nervous system; thus it has supervened upon the ingestion of a large quantity of cold water into the stomach.

841. Somatic Death may be occasioned, *secondly*, by an obstruction to the flow of blood through the capillaries of the lungs, constituting *Asphyxia* (§ 299); and this may be consequent upon a disordered state of the lungs themselves, or upon suspension of the respiratory movements through affections of the Nervous centres. It is in this mode that most fatal disorders of the Nervous System produce death, except when a sudden and violent impression occasions a cessation of the heart's power; thus in Apoplexy, Narcotic Poisoning, &c., death results from the paralyzed condition of the Medulla Oblongata; whilst in Convulsive diseases, the fatal result generally ensues upon a spasmodic fixation of the respiratory muscles.—*Thirdly*, Somatic death may be occasioned by a disordered condition of the *Blood* itself, which at the same time weakens the power of the Heart, impairs the activity of the Nervous system, and prevents the performance of those changes in the systemic Capillaries, which afford a powerful auxiliary to the circulation. This is death by *Necræmia*.*—*Fourthly*, Somatic death may result directly from the agency of *Cold*, which stagnates *all* the vital operations of the system. Where the cooling is due to the agency of an extremely low external temperature, which acts first upon the superficial parts, there is reason to think that the congestion of the internal vessels thereby induced occasions a torpid condition of the Nervous centres, and that the cessation of the Circulation is immediately due to Asphyxia. But when the cooling is gradual, and the loss of heat is almost equally rapid throughout, it is obvious that the stagnation must be universal, and that no cessation of activity in any one part is the occasion of the torpor in the functions of the remainder. It is in this manner that death ordinarily results from Starvation, and not by the weakening of the heart's action, as commonly supposed; the proofs of this have been already stated (§ 389).

842. As a general rule, we find that the more active the changes which normally take place in any tissue during life, the more speedily does its *Molecular* Death follow Somatic Death, the requisite conditions of its vital action being no longer supplied to it. Thus we observe that in Cold-blooded animals, the supervention of Molecular upon Somatic death is much less speedy than it is in Birds and Mammals. This seems due to two causes. In the first place, the tissues of the former, being at all times possessed of a lower degree of vital activity than those of the latter, are disposed to retain it for a longer time; according to the principle already laid down. And secondly, as the maintenance of a high temperature is an essential condition of the vital activity of the tissues of Warm-blooded animals, the rapid cooling of the body after Somatic death is calculated to extinguish it speedily; and that this cause has a real operation, is evinced by the influence of artificial warmth in sustaining the vital properties of separated parts.—The rapidity, however, with which Molecular death follows the cessation of the general circulation, will be influenced by a variety of causes; but especially by the degree in which the condition of the solids and fluids of the body has been impaired by the mode of death. Thus in Necræmia, Asthenia, and death by gradual cooling, Molecular and Somatic Death may be said to be simultaneous; and the same appears to be true of death by sudden and violent impressions on the Nervous system (§ 227). But in many cases of death by causes which operate by producing a more gradual Syncope or Asphyxia, the

* See Dr. C. J. B. Williams's "Principles of Medicine," 3rd edit., p. 553.

tissues and blood having been previously in a healthy condition, Molecular death may be long postponed; and we cannot be quite certain that it has supervened until signs of actual decomposition present themselves.

843. When Molecular death takes place in an isolated part, it must result from some condition peculiar to that part, and not primarily affecting the body in general. Thus we may have Gangrene or Mortification of a limb as a direct result of the application of severe cold, or of an agent capable of producing chemical changes in its substance, or of violent contusions occasioning mechanical injury; or, again, from an interruption to the current of nutritive fluid; or, further, from some ill-understood stagnation of the nutritive process, which manifests itself in the spontaneous death of the tissues without any assignable cause, as in some cases of senile gangrene. Sometimes we are enabled to trace this stagnation to a disordered condition of the circulating fluid; as in the gangrene resulting from the continued use of the 'ergot' of rye or wheat; but we can give no other account of the almost invariable commencement of such gangrene in the extremities, than we can of the selection of lead, introduced into the blood, by the extensors of the fore-arm.—If Mortification or Molecular Death be once established in any part, it tends to spread, both to contiguous and to distant portions of the body. Thus we have continually to witness the extension of gangrene of the lower extremities, resulting from severe injury or from the use of the ergot, from the small part first affected, until the whole limb is involved; and this extension is easily accounted for, by our knowledge of the tendency of organic substances in the act of decomposition to produce a similar change in other organic substances subjected to the influence of proximity to them. And the propagation of the gangrenous tendency to remoter parts is obviously due to the perversion of the qualities of the Blood, which results from a similar cause.*

844. It is quite certain that an *apparent* cessation of *all* the vital functions may take place, without that entire loss of vitality which would leave the organism in the condition of a *dead* body, liable to be speedily disintegrated by the operation of chemical and physical agencies. The state of Syncope is sometimes so complete that neither can the heart's action be perceived nor any respiratory movements be observed, all consciousness and power of movement being at the same time abolished; and yet recovery has spontaneously taken place, which could scarcely have been the case if *all* vital action had been suspended.—It is not a little remarkable, that certain individuals have possessed the power of *voluntarily* inducing this condition. The best authenticated case of this kind is that of Col. Townsend, which was described by Dr. George Cheyne,† who was himself the witness of the fact. But statements have also been made respecting the performances of certain Indian Fakeers, which are far more extraordinary; it being demonstrated, if these assertions are to be credited,‡ that the Human organism may not only be

* On the proximate causes of Death, see especially the Art. 'Death,' by Dr. Symonds, in the "Cyclop. of Anat. and Phys.," vol. i.; the first chapter of Prof. Alison's "Outlines of Pathology and Practice of Medicine;" and Dr. C. J. B. Williams's "Principles of Medicine," 3rd edit., pp. 536–557.

† See his "Treatise on Nervous Diseases," p. 307.

‡ See a collection of these cases, directly obtained from British officers who had been eye-witness of them in India, by Mr. Braid, in his "Observations on Trance, or Human Hybernation," 1850.—In one of these, vouched-for by Sir Claude M. Wade (formerly political agent at the Court of Runjeet Singh), the Fakeer was buried in an underground cell, under strict guardianship for *six weeks*; the body had been twice dug up by Runjeet Singh during the period of interment, and had been found in the same position as when first buried.—In another case, narrated by Lieut. Boileau in his "Narrative of a Journey in Rajwarra, in 1835," the man

voluntarily reduced to a state resembling profound collapse, in which there appears to be nearly a complete suspension of all its vital operations, but may continue in that condition for some days or even weeks, until, in fact, means are taken to produce resuscitation.—Another form of apparent death, the existence of which appears to be well-authenticated, is that sometimes designated as 'Trance' or 'Catalepsy,' in which there is a reduction of all the Organic Functions to an extremely low ebb, but in which Consciousness is still preserved, whilst the power of voluntary movement is suspended; so that the patient, though fully aware of all that is being said and done around, is unable to make the least visible or audible sign of life.* It is impossible, in the present state of our knowledge, to give any satisfactory account of these states; but some light appears to be thrown upon them by certain phenomena of artificial somnambulism, 'hypnotic' or 'mesmeric' (§ 539); for, in this condition, there is sometimes an extraordinary retardation of the respiratory movements and of the pulsations of the heart, which, if carried farther, would produce a state of complete collapse; and its self-induction is suspected by Mr. Braid to be the secret of the performance of the Indian Fakeers just referred to.

845. The signs by which *real* is certainly distinguishable from *apparent* Death, are not numerous, a large proportion of those commonly relied on being fallacious; but they are conclusive.—In the first place, it is to be remarked that no reliance is to be placed, for the reasons already mentioned, upon the apparent cessation of the Heart's action and of the Respiratory movements; since the reduction of these to so low a condition that they are no longer distinguishable, is by no means incompatible with the persistence of vitality. It has been suggested, however, that the persistence of the circulation in its feeblest degree may be rendered manifest by the application of a ligature to a finger, which may become swollen on the distal side if the heart still continues to act.† A surer test, however, is afforded by the condition of the *Muscular* substance; for this gradually loses its irritability after real Death, so that it can no longer be excited to contraction by electrical or any other kind of stimulation; and the loss of irritability is succeeded by the appearance of cadaveric rigidity. So long, then, as the muscle retains its irritability and remains free from rigidity, so long we may say with certainty that it is *not dead;* and the persistence of its vitality for an unusual period affords a presumption in favour of the continuance of some degree of vital action in the body generally; whilst, on the other hand, the entire loss of

had been buried for ten days in a grave lined with masonry and covered with large slabs of stone, and strictly guarded; and he assured Lieut. Boileau that he was ready to submit to an interment of a twelvemonth's duration if desired.—In a third case, narrated by Mr. Braid, the trial was made under the direct superintendence of a British officer, a period of nine days having been stipulated-for on the part of the devotee; but this was shortened to three at the desire of the Officer, who feared lest he should incur blame if the result was fatal.—The appearance of the body when first disinterred, is described in all instances as having been quite corpse-like, and no pulsation could be detected at the heart or in the arteries; the means of restoration employed were chiefly warmth to the vertex and friction to the body and limbs.—It may be remarked that the possibility of the protraction of such a state (supposing that no deception vitiates the authenticity of the narratives referred to) can be much better comprehended as occurring in India than as taking place in this country; since the warmth of the tropical atmosphere and soil would prevent any serious loss of heat, such as must soon occur in a colder climate, when the processes whereby it is generated are brought to a stand.

* Several such cases are recorded in Dr. H. Mayo's "Letters on the Truths contained in Popular Superstitions," and also by Mr. Braid, op. cit.

† See also Norris, Humphry and Turner's "Journal of Anat. and Physiology," vol. i. p. 217.

irritability, and the supervention of rigidity, afford conclusive evidence that death has occurred. The most satisfactory proof, however, is given by the occurrence of *putrefaction;* this usually first manifests itself in the blue-green coloration of the cutaneous surface, especially the abdominal; but it speedily becomes apparent in other parts, its rate being usually in some degree of accordance with the external temperature, though also much influenced by the previous condition of the solids and fluids of the body, these having been sometimes left by diseased actions in a state that renders them peculiarly prone to disintegration.

846. With the final restoration of the components of the Human Organism to the Inorganic Universe, in those very forms (or nearly so) in which they were first withdrawn from it, the Corporeal Life of Man, of which it has been the object of the foregoing Treatise to sketch the leading features, comes to a final close. But the Death of the Body is but the commencement of a new Life of the Soul; in which (as the religious physiologist delights to believe) all that is pure and noble in Man's nature will be refined, elevated, and progressively advanced towards perfection; whilst all that is carnal, selfish, and degrading, will be eliminated by the purifying processes to which each individual must be subjected, before Sin can be entirely subjugated, and Death can be completely "swallowed up of Victory."

APPENDIX.

Composition of BONE :—

	Per Cent.
The bones of a 3 days old child lost by incineration	38·81
14 „ „ (bones of skull)	35·33
„ „ „ (femora)	32·47
6 years old „ compact bone of diaphysis . .	34·49
„ „ „ cortical layer of epiphysis . .	36·84
Woman, æt. 22, compact substance of femur . .	35·4
„ „ 80 „ „ . .	35·4

The Residue of bone after incineration was found by Heintz to contain, per cent. :—

	I.		II.
Ca	38·59	...	38·56
PO_4	53·75	...	53·87
CO_2	5·44	...	5·51
Fl	1·74	...	1·58
Mg	0·48	...	0·48

Dry dentine of the ox was found by Aeby to contain :—

PO_4, 40·47 per cent. ; CO_2, 0·97 ; Ca, 28·74 ; Mg, 0·15. Organic compounds, 27·70 per cent., with traces of iron and sulphuric acid. The ivory contained PO_4, 55·15 per cent. ; CO_2, 3·32 ; Ca, 37·28 ; Mg, 0·21. Organic substances, 3·60.

Composition of Mixed SALIVA :—

Water	994·10	...	995·16	...	994·698
Solids	5·90	...	4·84	...	5·302
Soluble organic compounds.	1·42	...	1·34	...	3·271
Epithelium	2·13	...	1·62	...	?
Potassium sulphocyanide .	0·10	...	0·06	...	?
Inorganic salts	2·19	...	1·82	...	1·031

The composition of the secretion of the submaxillary gland in the dog is thus given by Herter :*—

	I.		II.		III.
Water	994·385	...	995·411	...	991·319
Solids	5·615	...	4·589	...	8·681
Organic substances	1·755				
Of which Mucin constituted .	0·662	...	—	...	2·604
Inorganic salts (soluble) . . .	3·597	...	—	...	5·209
„ (insoluble) . .	0·263	...	—	...	1·123
Chemically combined CO_2 . .	0·440	...	0·654		

I. and II. were obtained by stimulating the mouth with vinegar, and III. by giving meat to eat.

* Hoppe-Seyler, "Phys. Chem.," p. 191 (1878).

The composition of the secretion of the parotid gland of the dog is, according to Herter :*—

Water	993·849	991·527	991·928
Solids	6·151	8·473	8·072
Organic substances .	—	1·536	
K.S.C.N. K Cl. Na Cl. . . .	—	6·251	
Ca CO_3	—	0·688	

Composition of the GASTRIC JUICE OF MAN :—

Water	994·404
Organic constituents . . .	3·195
H Cl	0·200
Ca Cl_2	0·061
Na Cl	1·465
K Cl	0·550
Ca_3 2(PO_4) Mg_3 2 PO_4 Fe PO_4	0·125

Composition of the PANCREATIC JUICE :—

Of Dog—Schmidt.		Of Horse—Hoppe-Seyler.	
Water	900·76	Albumin . .	0·22 per 1000
Solids	90·38	Ferment . .	8·657
Ashes	8·54	Soluble salts .	0·389
		Water . . .	982·530

From permanent fistula of the pancreatic duct in dog (Kröger) :—

Water	976·780	to	984·630
Organic substances	16·390		9·210
Salts	6·833		6·159

The composition of LYMPH *is* :—

	Gubler and Quevenne.		Scherer.	Hensen and Dähnhardt.			
	I.	II.	III.	IV.	V.	VI.	VII.
Water . . .	939·9	934·8	957·6	987·7	—	986·126	985·201
Solids . . .	60·1	65·2	42·4	12·3	—	13·874	14·799
Fibrin . . .	0·5	0·6	0·4		1·070		
Globulin . . Serum albumin	42·7	42·8	34·7	2·6	0·894 1·408	3·811	6·875
Fat, cholesterin, and lecithin .	3·8	9·2	?	0·03	—		
Extractives . .	5·7	4·4	?	1·28	—		
Salts	7·3	8·2	7·2	8·38	—	10·06	7·926

* Hoppe-Seyler, *op. cit.*, p. 199.

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